

SOME AMERICAN CARBONIFEROUS FERN FRUCTIFICATIONS¹

SERGIUS HARRY MAMAY²

INTRODUCTION

Prior to the discovery of coal balls and the development of techniques which made possible the cutting of petrifications for detailed anatomical studies, the attention of paleobotanists was mostly limited to considerations of impressions and compressions. The resultant early studies demonstrated that certain plants which bore fern-like foliage, often preserved in exquisite fashion, constituted conspicuous elements in the Coal Age floras of Europe and America. To Adolph Brongniart falls the bulk of the credit in the nomenclature of these foliar compressions.

At an early date fertile specimens bearing circular groups of sporangia upon the lower surfaces were found among the fern-like leaf impressions. Such specimens, the majority of which were referable to the genus *Pecopteris*, were, by virtue of what information could be gathered from the compressed fructifications, commonly regarded as constituting a marattiaceous element in the Coal Age floras. This opinion met with little controversy until the early part of the 20th century, when it was demonstrated that at least some of the Carboniferous plants to which fern-like foliage was attributed bore seeds. This initiated our knowledge of the pteridosperms, an extremely interesting group which has since been much investigated. While some authors preferred to look with doubt upon the marattiaceous affinity of the pecopterid fructifications, the striking anatomical similarity of the fossil stem *Psaronius* to the living marattiaceous genus *Angiopteris*, along with other factors, appeared to strengthen the validity of the Carboniferous Marattiaceae, despite the supposed likenesses between the pecopterid fructifications and certain of the pteridospermous microsporangiate fructifications.³

Anatomical studies of coal ball plants, begun in England in 1868 by Binney and further pursued by such outstanding anatomists as Williamson and Scott, demonstrated the presence of an additional complex in the Carboniferous floras, the primitive ferns or Coenopterideae (Seward, 1910). Although these plants are yet incompletely known, the nature of their vascular systems and fructifications indicates affinities with certain of the ferns rather than with other vascular cryptogams.

In spite of the fact that investigations of coal balls in America have been under way for only two decades, we have achieved at least an introductory picture of our Coal Age floras. Numerous coal ball localities have been discovered in Illinois, Iowa, Indiana, and Kansas, with the result that significant literature has accumu-

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²John Simon Guggenheim Fellow, University of Cambridge, England, 1950-51.

³This problem is considered in greater detail in the summary.

lated.⁴ It is known that American Carboniferous floras contained liberal representatives of the Marattiaceae, Pteridospermae, and Coenopterideae, and while considerable attention has been directed toward studies of the anatomy and fructifications of the American pteridosperms, much remains to be learned about the Marattiaceae and Coenopterideae, chiefly from the standpoint of their fructifications. A few brief descriptions of the vegetative organs and fructifications of these plants have been published, yet their abundance in recent collections indicates that this represents only a beginning toward a comprehensive knowledge of these elements of the American floras.

The scarcity of literature dealing with petrified fructifications might be explained thus: The organs in question are extremely small and rarely occur in sufficient quantities to constitute conspicuous masses. The better-known descriptions have been based chiefly on remarkably large aggregations of fructifications such as *Botryopteris forensis* Renault and *B. globosa* Darrah. Such specimens are rare. To undertake a study of these organs involves painstaking systematic inspections of many petrifications under reasonably high magnification, a process which might easily be deferred in favor of investigation of larger, more conspicuous stems, seeds, etc.

The present paper treats the various fructification species present in coal balls from various American localities. These have been critically compared with descriptions of all related species from both Europe and America, with the result that several distinctly new entities are recognized. These include three new species of *Botryopteris* Renault; one new species of *Cyathotrachus* Watson, the generic concept of which is emended; three new species of *Scolecopteris* Zenker, and a new variety of *S. minor* Hoskins, in addition to an emendation of and supplementary data concerning *S. latifolia* Graham; and a new genus, *Eoangiopteris*, which is postulated as a progenitor of the *Angiopteris* type of modern marattiaceous sori.

In recognizing new species, the size of sporangia, structure of sporangial walls, and the number of sporangia in the fructifications are carefully considered as criteria, with critical attention given to the range of variation which might be expected within the limitations of a species. Where possible, details of the supporting pinnules are also noted. All these features appear to be trustworthy criteria for speciation, but it has been found that the spores present the single outstandingly dependable basis for comparison. While variation among the spores of the various species of a given genus is extreme, from the standpoints of both size and morphology (the spores of *Scolecopteris*, for instance, range from 10 to 80 μ in diameter, and may be of either bilateral or tetrahedral symmetry), they are remarkably constant among different specimens of a given species⁵; considering the spores together with the other variables mentioned above, a reliable concept of the species complex of a fructification genus may be arrived at.

⁴A comprehensive review of American coal ball literature, is being prepared by H. N. Andrews, for a future number of the 'Botanical Review.'

⁵In limiting the diagnostic value of these spores to the specific level we concur with Knox (1938) who wrote: ". . . and even for genera there are not many examples where spore characters could be held to be diagnostic."

The accepted practice of designating holotypes in describing new species of fossil plants is hardly practicable when dealing with fructifications as small as those involved in this study. With a stem specimen of a centimeter or so in diameter and several centimeters in length, it is possible to make sufficient sections to gain a thorough understanding of the specimen and still preserve enough material to constitute a holotype for future reference. However, the fructifications described in this paper scarcely exceed a single millimeter in length, making it impossible to arrive at a reconstruction from a single specimen. Fortunately, their smallness is generally compensated for by their abundance in the coal balls. In several cases, the initial cut of a coal ball has exposed numerous fructifications sectioned in all planes and levels. Thus we have been able to obtain a complete and accurate concept of the nature of a fructification species by examination of a single peel. In more critical studies of exceptional specimens, however, serial peel sections were employed. Since the descriptions of new species are based upon not one but several specimens, we will cite *syntypic* slides which have been made from peels selected because of their abundant fructification content or excellence of preservation, or both.

MATERIALS AND TECHNIQUES

At the beginning of this investigation, attention was concentrated on a collection of coal ball slabs from the Urbandale Mine near Des Moines, Iowa, particularly rich in fern fructifications, and it was in them that the majority of the specimens described were found. This material was generously donated to the Washington University collection by Mr. Frederick O. Thompson of Des Moines, whose collecting activities during the past several years have indeed proven a boon to recent American paleobotanists.

As the investigation proceeded, coal balls from various other localities were collected and inspected. Those which have produced fructification material are:

1. The Urbandale Mine, located 1.2 miles west of Des Moines, Iowa, on U. S. Highway #6 (Walnut Township, Dallas County). This coal lies in the Des Moines Series of the Pennsylvanian. (See Andrews and Kernen, 1946.)

2. Berryville, Illinois. This small outcrop, which is found in a stream bed approximately 2 miles northeast of Berryville, Illinois (Sumner Quadrangle, Lawrence County), lies in the upper portion of the McLeansboro Group of the Pennsylvanian of Illinois.

3. Big Creek #1 Mine of the Wasson Coal Mining Corporation, which is located approximately 2 miles south and 1.5 miles east of Lynnville, Indiana. This coal (Petersburg V) lies in the upper portion of the Des Moines Series.

4. Strip pits of the Pittsburgh and Midway Coal Company, located 4 miles south of Mineral, Kansas (Columbus Quadrangle, Cherokee County). This coal is known as the Fleming Coal, and lies in the upper one-third of the Cherokee Shale, which is found in the Des Moines Series of the Pennsylvanian.

5. Shore, Lancashire, England. The material from this locality consists of a single small coal ball fragment. This coal seam lies in the Great Coal Ball Horizon of the Lanarkian Series. (See Schopf, 1941.)

While each of these localities has produced fern fructifications in some abundance, none has approached the Urbandale for the number of species present. However, at the time of this writing, the Mineral, Kansas, material is only beginning to be investigated, but it promises to equal or even surpass the Urbandale locality in diversity of the flora.

The peel technique followed is essentially that outlined by Pannell (1942). In a few instances it was necessary to make successive peels at intervals as close as possible, due to the smallness of the specimens. Those specimens selected for illustrative purposes were cut from the peel, mounted in Clarite on glass slides, and photographed with Panatomic X sheet film and a green Wratten filter.

All the slides cited are catalogued in the Washington University paleobotanical collection.

COENOPTERIDALES

While much is known of the vegetative anatomy of the coenopterids, or primitive ferns, relatively little is known of their fructifications. The various genera are easily distinguished on the basis of their petioles, which exhibit great diversity of structure, in contrast to the generally simple and uniform organization of the stems. Although considered to be an extremely primitive group of vascular plants, they nevertheless embrace genera with certain structural modifications suggestive of higher groups, e. g., the axillary branching of *Ankyropteris*, the weak but distinct secondary thickening in the stem of *Botrychioxylon*, and the compact, synangial fructifications of *Chorionopteris*, which were borne on well-developed laminae.

Regarding the fructifications, the diversity of structure within the coenopterids is great. In the most primitive representative, *Stauropteris*, the sporangia are solitary, exannulate, massive-walled, and borne terminally on the ultimate ramifications of the radially symmetrical "frond." Between this extreme and that seen in *Chorionopteris*, various intermediate forms are known (this series is considered more critically in the conclusion of this paper). The extremely diverse structure of the petioles, the axillary branching, and the cambial activity, prompt the conclusion that the coenopterid ferns must have constituted an extremely plastic evolutionary plexus from which several lines of fern (and probably pteridosperm) development began to emerge early in the history of vascular plants. The appearance in the late Paleozoic of fern fructifications which show strong affinities with the Schizaeaceae (*Senftenbergia*), Gleicheniaceae (*Oligocarpia*), and Marattiaceae (*Scolecopteris*, *Cyathotrachus*, etc.), along with stem remains whose anatomy indicates osmundaceous affinity (*Thamnopteris*, *Zallesskya*), appears to strengthen such a supposition. This would also seem to imply an extremely early differentiation of both the eu- and leptosporangiate development of fructifications, very

likely much earlier than the development of laminate foliar organs.

The vegetative remains of several coenopterid genera have been reported in American paleobotanical literature.⁶ Stems and petioles of *Ankyropteris*, *Botryopteris*, *Etapteris*, *Stauropteris*, *Anachoropteris*, and *Grammatopteris*⁷ have been reported in America. However, only the genus *Botryopteris* is known from its fructifications, these having been reported by Darrah (1939) and Graham (1935). Graham also described a new fructification genus of apparently coenopterid affinity, but which has not been correlated with any stem genus (*Notoschizaea robusta*). He pointed out a strong resemblance of *Notoschizaea* to the fructification *Corynepteris*, however.

The coenopterid fructifications found during this investigation are representatives of the genus *Botryopteris* Renault, the vegetative organs of which are found in some abundance in American coal balls. The history of the fructification species of *Botryopteris* follows:

BOTRYOPTERIS Renault, Ann. Sci. Nat. (Bot.) VI, 1:223–229. 1875.

Renault's type species, *B. forensis*, was based upon silicifications from the Permo-Carboniferous of Autun and St. Etienne. Renault was fortunate in finding both the vegetative organs and the fructifications, with no reason for doubt as to the correlation between the two. The sporangia were produced in small clusters on the termini of the ultimate ramifications of a much-branched "frond," resulting in a large compound fructification containing possibly several thousands of sporangia. The individual sporangia are shortly pedicellate, more or less pyriform, and attain lengths of 2 mm. and diameters of 1 mm. The sporangial walls are, according to Renault, ". . . formées d'un seul rang de cellules polyédriques . . .", and are distinctive in possessing a multiseriate annulus-like band of enlarged cells which extends from the apex to the base along one side of the sporangium. Dehiscence occurred by a longitudinal cleft along the thin opposite wall. The spores are spherical, apparently smooth-walled, and attain diameters of 70 μ .

In the same publication Renault described a second species of *Botryopteris* (*B. dubius*) which he later transferred to the genus *Zygopteris*.

Scott (1910) described a group of sporangia from the Lower Carboniferous of Pettycur, which was found in intimate association with a petiole of *B. antiqua*. The sporangia measure from 240 to 280 μ in diameter, with the cells of the annulus reaching 60 μ in diameter. The spores average 25 μ in diameter, and are somewhat triangularly flattened. A structure which he interpreted as of possible indusial nature was found associated with the sporangia. Scott (1920) has also reported similar small botryopterid sporangia in association with the Lower Carboniferous species *B. hirsuta* and *B. ramosa*.

Graham (1935) described botryopterid petioles and sporangia from the Upper Pennsylvanian of Illinois, naming them *B. americana*. Among the fructifications

⁶Darrah (1941) has summarized the American coenopterids.

⁷An excellent specimen of *Grammatopteris* has only recently been found by us in a coal ball from Berryville, Illinois. This is apparently the first known occurrence of this genus in this country.

he noted "sterile" sporangia which he termed "specialized" without further elaboration. Dimensions are not cited, but judging from the size of the drawings and the magnifications given the sporangia appear to be approximately .70 mm. wide and 1.30 mm. long, with spores about 30 μ in diameter.

The second American species, *B. globosa* Darrah (1939), is from the Upper Pennsylvanian of Iowa. This remarkable fructification is the American counterpart of Renault's *B. forensis*, consisting of innumerable sporangia borne in terminal tufts on a highly branched "frond."

During the present investigation *Botryopteris* fructifications have been found in coal balls from the Urbandale Mine, Iowa, and Berryville, Illinois. These are much smaller than previously described species, with the exception of those reported by Scott. Although they do not differ greatly among themselves in sporangial dimensions, three distinct species are recognized, based chiefly on spore morphology.

BOTRYOPTERIS fecunda, sp. nov. (figs. 1-4).

Numerous clusters of small sporangia are present in coal balls # 437A, 442, 679, and 680, from the Urbandale mine. Their compact aggregation in all cases suggests that these clusters represent small portions of highly compound fructifications comparable in complexity to those of *B. forensis* and *B. globosa* (fig. 3). It is apparent that each cluster consists of from 5 to 20 sporangia, terminating small frond ramifications. The attachment to these ultimate branchlets has only been noted in a few isolated cases, the branchlets themselves being very poorly preserved.

The individual sporangia are shortly pedicellate, and ovoid-ellipsoid in longitudinal section (fig. 1); in transverse section perfectly oval (fig. 2). The sporangia reach a maximum of .45 mm. in length and .25 mm. in diameter.

The sporangial walls are but a single cell thick. As seen in transverse section, the wall displays a differential thickening which served as an annulus. The largest cells of the annulus are approximately 50 \times 50 μ in their transverse dimensions and about 75 μ in length. Their inner and radial walls are thicker than the free outer walls. The size of the cells decreases gradually, with the smallest cells measuring only 8-10 μ in thickness. Dehiscence occurred by means of a longitudinal cleft along the thinnest portion of the wall. The differential thickening of the sporangial wall may be clearly seen in figs. 1 and 2.

Numerous well-preserved spores are present in nearly every sporangium. They are of radial-trilete morphology (see fig. 4). The commissural, or inner surfaces, of the spores are compressed into three nearly equilateral triangular surfaces, each measuring about 36 μ along its basal side. The inner sides are delimited by a prominent triradiate ridge which extends nearly to the corners of the inner face. The spore walls are finely reticulate, the differential thickening producing extremely thin and translucent spots between the thickened ridges.

The small size of the sporangia and the distinctness of the spores warrant recognition of this fructification as a new species. The specific name *fecunda* is

proposed in reference to the prolificity with which the sporangia were produced.

Specific Diagnosis: Sporangia borne in compact terminal clusters of 5 to 20 each, pedicellate, ovoid-ellipsoid, reaching .45 mm. in length and .25 mm. in width. Largest cells of annulus averaging $50 \times 50 \mu$ in transverse dimensions. Spores radial, trilete, averaging 36μ along the base of each triangular commissural surface, and with pronounced triradiate ridges; spore walls finely reticulate, with thin, translucent areolae.

Age: Des Moines Series of the Pennsylvanian.

Locality: Urbandale Mine, Iowa.

Type Slides: #1676-1680.

BOTRYOPTERIS spinosa, sp. nov. (figs. 5-8).

A single group of rather loosely aggregated sporangia with dimensions similar to those of *B. fecunda*, but of slightly different shape and with entirely distinct spores, was found in WCB 437B, from the Urbandale mine (fig. 6). The sporangia are much more loosely arranged than those of *B. fecunda*. The pedicellate attachment to a small ultimate rachis was clearly observed in one case (fig. 7). The sporangia average .50 mm. in length and .25 mm. in diameter. In longitudinal section they are somewhat narrowed at the base, resulting in a pyriform aspect. The sporangial walls are a single cell thick. The largest cells of the annulus measure approximately $50 \times 50 \mu$ in transverse dimensions and 70μ in length (fig. 8).

The spores (fig. 5) are perfectly spherical, averaging 45μ in diameter. A faint triradiate ridge is present, each leg not exceeding 10μ in length. The spore walls are smooth, but distinct in being sparsely studded with blunt spines reaching 6μ in length and averaging 2μ in diameter. Calculations indicate a comparatively low spore output, not exceeding a hundred spores per sporangium.

This species is named *spinosa* with reference to the spinose ornamentation of the spore walls.

Specific Diagnosis: Sporangia borne in loosely aggregated clusters terminating the ultimate ramifications, shortly pedicellate, pyriform, averaging .50 mm. in length and .25 mm. in diameter. Largest cells of annulus averaging $50 \times 50 \mu$ in transverse dimensions. Spores spherical, trilete, averaging 45μ in diameter, with faint triradiate ridges; spore walls sparsely provided with blunt spines reaching 6μ in length and 2μ in diameter.

Age: Des Moines Series of the Pennsylvanian.

Locality: Urbandale Mine, Iowa.

Type Slides: #1681-1683.

BOTRYOPTERIS illinoensis, sp. nov. (figs. 9, 10).

This description is based upon numerous isolated sporangia and one small cluster of eight, found in WCB 714 and 715, from Berryville, Illinois.

The sporangia are nearly spherical (fig. 10). The sporangial walls are a single cell thick, with the largest cells of the annulus measuring approximately 70μ radially and 40μ tangentially. No evidence of a sporangial pedicel has been observed.

The spores are quite distinctive (fig. 9). They are radial and trilete, with axial dimensions much smaller than the transverse. This is not due to crushing, however, as the spore walls are always fully distended. As seen in the transverse plane, the spores are roughly triangular, with rounded corners and markedly concave sides. The distance between corners averages 23μ ; the distance between one corner and the opposite concavity in the spore wall averaging 18μ . The rounded tips average 10μ in width. In axial dimensions the spores average 10μ . The walls are thin, with a faint triradiate ridge, the legs of which extend approximately two-thirds of the distance to the tips of the lobes. Otherwise there are no distinct markings on the walls.

Although this fructification is entirely distinct from all other American fructification species of *Botryopteris*, it corresponds quite closely to those reported by Scott (1910) in association with the English species *B. antiqua*, *B. hirsuta*, and *B. ramosa*. However, the absence of these species in American coal balls and their greater geological age make it seem quite unlikely that the fructifications are conspecific with the Illinois specimens. Furthermore, the Berryville locality has produced to date two stem species of *Botryopteris*,⁸ either of which may ultimately prove to have borne these sporangia. For this reason, in addition to the contrasting characters found between the Illinois specimens and all other American species, this fructification is recognized as an additional new species, the name *illinoensis* being proposed in recognition of its place of origin.

Specific Diagnosis: Sporangia ovoid, averaging .40 mm. in length and .30 mm. in diameter. Largest cells of the annulus averaging $70 \times 40 \mu$ in transverse dimensions. Spores radial, trilete, axially flattened, with rounded corners and concave sides, 10μ in axial dimensions and 23μ between corners; spore walls smooth, with faint triradiate ridges.

Age: McLeansboro Group of the Pennsylvanian.

Locality: Berryville, Illinois.

Type Slides: #1684-1686.

A comparison of the various species is presented in tabular form on the following page.

DISCUSSION

The sporangia discussed in the preceding pages, while belonging to an archaic fern genus, are striking in several respects. They have very delicate sporangial walls, a single cell thick. There is a differential thickening of the wall, suggestive of a primitive annulus. The sporangia themselves are very small, comparing closely with living osmundaceous sporangia in size. Finally, in at least the one species *Botryopteris spinosa*, spore output is relatively low, closely comparing to the Osmundaceae in this respect also.

While the coenopterid ferns have been variously known as the Primofilices (Arber, 1906), Coenopterideae (Seward, 1910), and Inversicatenales (P. Bertrand,

⁸In a recent communication, Dr. W. N. Stewart, of the University of Illinois, reported having found specimens of *B. radiata* Darrah in Berryville material. This locality is also the source of a yet unpublished new species of *Botryopteris*.

1909), they have invariably been considered as *eusporangiate* forms. As defined by Goebel (1880), one of the implications of this term is a sporangial jacket more than one cell thick. In this consideration alone the sporangia of *Botryopteris* fail to conform to the eusporangiates. While it is true that the bulky walls of sporangia of *Etapteris*, *Chorionopteris*, and *Stauropteris* allow no alternative but to consider the genera to be of eusporangiate nature, the thin-walled sporangia of *Botryopteris*, pointed out by Renault in his original description of the fructifications and by Scott and Bower, seem to offer grounds for doubting the validity of such an arbitrary scheme of classification.

COMPARISON OF THE VARIOUS FRUCTIFICATION SPECIES OF *BOTRYOPTERIS*

Species	Sporangial dimensions	Spore size	Spore morphology	Spore ornamentation
<i>B. forensis</i> Renault	1 × 2 mm.	70 μ	Spherical, trilete	Apparently smooth
<i>B. americana</i> Graham	1.30 × .70 mm. (?)	30 μ (?)	?	?
<i>B. globosa</i> Darrah	1.50 × 1 mm.	50–65 μ	Spherical, trilete	Smooth
<i>B. sp.</i> Scott	.28–.24 mm. diameter	25 μ	Triangularly flattened	?
<i>B. fecunda</i> Mamay	.45 × .25 mm.	36 μ along one side	Tetrahedrally compressed	Finely reticulate
<i>B. spinosa</i> Mamay	.50 × .25 mm.	45 μ	Spherical, trilete	With blunt spines
<i>B. illinoensis</i> Mamay	.40 × .30 mm.	23 μ between lobes	Axially flattened, triangular, with concave sides	Smooth

Hirmer (1927), although adhering rigidly to the eusporangiate concept of the coenopterids, has taken a forward step in introducing a scheme of fern classification in which the Osmundaceae are placed in a position intermediate between the Leptosporangiatae and Eusporangiatae, the subdivision to which they are assigned (Protoleptosporangiatae) enjoying equal rank with the Eu- and Leptosporangiatae. The genus *Botryopteris* cannot be conclusively assigned to either of these two main groups, in view of the admixture of both primitive and advanced characters. It is highly probable that as our knowledge of the fossil ferns advances, the coenopterids eventually will be considered to be less closely interrelated than they have been previously, and that the great structural differences to be found among their fructifications will gain recognition in a revised classification.

MARATTIALES

This order, embracing a single family with seven living genera and a large complex of extinct forms, is characterized by its eusporangiate, exannulate fructifications consisting of more or less synangial, clearly circumscribed sori which are borne superficially.

The majority of the Carboniferous Marattiaceae bore radially symmetrical sori, and as has been pointed out previously by Hoskins (1926) and Graham (1934), these fructification genera were placed by Stur (1883) in a suborder of the Marattiales, the Asterotheceae. This suborder includes only fossil forms, now totaling six genera, two of which (*Scolecopteris* Zenker and *Cyatbotrachus* Watson) have been found to occur rather abundantly in the American coal balls investigated in this study. In addition to these two genera, whose histories are reviewed in succeeding pages, the Asterotheceae include the following:

Acitbeca Schimper: Synangia sessile; sporangia attached at their bases to a central column, with distal portions free; sporangial apices long and bristle-like. (For historical details see discussion of *Scolecopteris*.)

Asterotheca Presl: Synangia sessile; sporangia attached to a central receptacle, but free distally, their long axes parallel to the plane of the pinnule. Genus founded by Presl (Corda, 1845), and originally considered to be gleicheniaceus by Corda. Several species known, chiefly from compression material.

Ptychocarpus Weiss: Synangia pedicellate; sporangia enclosed in a continuous synangial sheath, and fused to a central column extending through the entire length of the synangium. Genus founded in 1869; the best-known description is that of *P. unita* Brongniart, by Renault (1896). (See fig. 11.)

Sturiella Weiss: Synangia pedicellate; sporangia basally fused but free above, each sporangium with an apical annulus-like structure. Genus founded by Weiss (Zeiller, 1890); a detailed description presented by Renault (1883) as *Pecopecteris intermedia*. The presence of the annulus-like structure, along with the synangial nature of the fructification, has caused *Sturiella* to be regarded as intermediate between the Marattiaceae and Osmundaceae.

These genera are limited mainly to strata of Upper Carboniferous age, and are all known to exist in organic connection or intimate association with foliage of the *Pecopecteris* type.

Although many of the petrifications investigated in this study contain an abundance of fructifications belonging to several genera, *Asterotheca* and *Ptychocarpus* are totally lacking. While petrified specimens of these two genera have been reported in the literature, they are represented in large part by compressed specimens. This situation suggests a problem in preservation phenomena.

It has been pointed out by Kidston (1925) and Arnold (1947) that the single major difference between *Scolecopteris* and *Asterotheca* lies in the fact that the former is pedicellate, the latter sessile. In all other features, such as size and shape of the sporangia and manner of dehiscence, they are essentially alike. Studies of petrified *Scolecopteris* specimens have shown that with maturity the sporangia be-

came radially extended from each other, much as the ribs of an opening umbrella; in this condition they closely approach the typical aspect of *Asterotheca*, discounting their pedicellate nature. If sufficiently extended prior to compression, the fructifications would eventually be preserved with the sporangia arranged in a typical asterothecoid fashion, with the pedicel totally obscured from view. There would thus be no dependable method of determining the true generic affinity of the specimen. Although it is not my intent to question the validity of the genus *Asterotheca*, the following pertinent facts should be given careful consideration:

1. Petrified fructifications referable to *Asterotheca* have not been recognized during this study,⁹ while *Scolecopteris* has been found in great abundance.
2. While the vast majority of accounts dealing with *Asterotheca* have been based on compression material, the exact reverse holds true for *Scolecopteris*.

Due to the reasons presented above it would appear that positive identification of compressed fructifications must not be made without careful consideration of the possibilities for generic confusion. A similar situation might exist in the genera *Ptychocarpus* and *Cyathotrachus*, which differ only in the extent of the central column, a feature which does not readily lend itself to accurate determination in the compressed form. While *Ptychocarpus* is found prolifically as compressions, in only two instances has it been reported in the petrified state in American literature.¹⁰ On the other hand, while three species of *Cyathotrachus* are known from petrifications, not a single compressed specimen has ever been reported, all compressed fructifications in which the sporangia are surrounded by a continuous synangial sheath being referred to *Ptychocarpus*.

CYATHOTRACHUS Watson, emend. Mamay.

C. ALTUS Watson, Roy. Micr. Soc. Jour. 1906. 1-3.

C. BULBACEUS Graham, Bot. Gaz. 95:459-461. 1934.

The genus *Cyathotrachus* is the most recent addition to Stur's (1883) Asterotheceae. Although the publication in which the genus was established appeared several years later than that of Stur, Graham (1934) was the first to recognize the asterotheceous affinity of the fructification and point out the necessity for including it within that group.

Watson's type species, *C. altus*, is from the Lower Coal Measures of England. His discovery of a cup-like tracheidal structure in the base of the synangium led to the adoption of the generic name *Cyathotrachus*. The specific name *altus* refers to the height of the fructification. Although his description does not include a clear statement of the generic characters, he apparently considered the tracheidal cup to be of primary importance. This concept has, however, been altered by subsequent discoveries. Graham, in describing the second species, *C. bulbaceus*, from the Upper Pennsylvanian of Illinois, failed to recognize any such structure

⁹Benninghoff (1943) briefly mentioned the presence of *Asterotheca* in Indiana coal balls.

¹⁰*Ptychocarpus* has been reported by Benninghoff (1943) and Hoskins (1933).

in his specimens and considered that its presence or absence could possibly constitute a generic difference. I have studied several scores of specimens from Iowa coal balls, paying particular attention to this detail, and I did not observe the tracheidal cup in a single fructification. Notwithstanding, there is ample evidence to support the belief that the two above-mentioned species and a third, described below, are congeneric. It appears that the fructification was inaptly named, since the generic name refers to an inconstant character which should be considered to be of only specific importance. The character of prime generic importance would seem to be the cup-like arrangement of the fructification itself.

An emended concept of the genus is presented in the following diagnosis:

Generic Diagnosis: Synangia pedicellate, circular, containing several more or less elongate, exannulate sporangia, the entire fructification enclosed in a continuous outer synangial sheath, with the exception of the apical pore. Basal portion of the synangium with a central column; apical portion hollow and cup-like.

CYATHOTRACHUS altissimus, sp. nov. (figs. 12–16).

The description is based upon numerous specimens scattered through several of the Urbandale coal ball slabs from the Thompson collection. Although usually occurring singly, a few specimens consisting of several closely associated synangia were found. In several instances it was possible to select specimens for further study with the naked eye, because of the large size of the fructifications and the characteristic bright golden color of their spore masses, which were in striking contrast with the less conspicuously colored matrix.

Although the number of sporangia in a synangium ranges from 5 to 9, those with 7 are predominant. The innermost walls of the sporangia are fused with the tissue of a central column¹¹ that extends slightly beyond the middle of the synangium. The column flares out somewhat at the distal end, forming a shallow saucer-like structure beyond which the synangium is hollow and resembles a deep cup. Proximally, the column extends beyond the bases of the sporangia to form the short synangial pedicel. The column is composed of elongate thin-walled cells averaging approximately 25 μ in diameter and 300 μ in length. There is no evidence of vascular elements in this structure.¹² Average dimensions of the central column are approximately .20 by .80 mm. (fig. 12).

Individual sporangia average 1.50–1.80 mm. in length and .20–.45 mm. in diameter, the radial dimensions being slightly greater than the tangential, due to lateral appression with adjacent sporangia. The synangia as a whole average .80–.90 mm. in diameter. Throughout the portion of the synangium that is traversed by the central column, the lateral walls of the sporangia are so closely appressed as to present the appearance of a single wall (fig. 15), but progressing distally beyond the termination of the column the walls of adjacent sporangia can

¹¹Watson (1906) termed this structure a "columella", but this usage is questionable, since the column is not, in this case, a structural entity of the sporangium proper.

¹²Watson (1906) found tracheids in this column, and Graham (1934) termed this tissue "transfusion tissue" without further elaboration.

be distinguished from each other. The character of the sporangial walls is best seen in dehiscent synangia (fig. 16). The cells are thin-walled, and there appears to be only one layer. The outer surface of the synangium is enclosed by a continuous layer of thin-walled cells corresponding very closely to the synangial wall found in *Ptychocarpus*. This layer of tissue partially fills the angles created where the lateral walls of adjacent sporangia depart from each other, and varies from one to three or four cells in thickness. Serial sections indicate that the synangial wall increases in thickness as the distal end of the synangium is approached. This structure is shown in fig. 13. The fact that it is not present in all specimens indicates that it may have been rather fragile tissue, probably drying at maturity and being either blown off by the wind or rubbed off by friction with adjacent synangia.

The cellular details of the pinnules were observed in a few isolated fragments. The upper epidermis is highly cuticularized and shows no cellular detail, being seen only as a dense black line. Beneath the palisade layer the cells are rather loosely aggregated and show no apparent differentiation, with the exception of the one or two lowermost layers of cells, which are flattened in the plane of the lamina surface. These appear to be a continuation of the pedicel, showing a close similarity to its tissue both in size and shape of cells. The pedicel is very short and thick, and the tissues composing it are not distinguishable from those of the central column. The manner in which the synangia were oriented upon the surface of the lamina was observed in one specimen. This consists of several distinct rows of compactly arranged synangia oriented at right angles to a structure which appears to be the midrib of a penultimate pinnule, two adjacent rows of synangia probably representing the fructifications produced by a single ultimate pinnule. Unfortunately, that portion of the coal ball containing the remainder of the specimen was not among the slabs presented by Mr. Thompson, and we have not been able to ascertain the relationship between the rows of synangia and the parent pinnules, or the nature of the pinnules. Since the two previous species are known to be in close association with *Pecopteris* foliage, and since the orientation of the synangia in this specimen seems to correspond closely with that of other asterotheceous pecopterid fructifications, it seems safe to assume that this species was borne on foliage of the *Pecopteris* type.

Neither Watson nor Graham described the dehiscence of *Cyatbotrachus*, but fortunately many of the Iowa specimens illustrate that feature very well. Dehiscence was accomplished by means of longitudinal slits along the inner walls of the sporangia, extending from the sporangial apices as far as the proximal limits of the hollow portion of the synangium. Although no specialized stomial or annulate structures were present, the inner surfaces of the sporangia, being the thinnest, offered the line of least resistance, with the results described here. Dehiscence of the sporangia was accomplished by a rupturing of the outer envelope of the synangium and separation of the closely appressed walls of adjacent sporangia; this release of both lateral and peripheral tension allowed the sporangia to

assume a more nearly cylindrical appearance than that displayed prior to dehiscence. That portion of the sporangium adjacent to the central column, however, was not altered by dehiscence; lateral walls remained closely appressed with those of the adjacent sporangia, and the synangial wall remained intact. Figure 15 shows a transverse section of a sporangium that has already shed its spores. Here the section has been taken through the central column, and the synangial wall is still a continuous tissue surrounding the entire structure. Dehiscence is further illustrated in fig. 16, in which the spores are being shed into the hollow synangial cup.

Spores of this species are small, with bilateral-monolete symmetry, averaging $12 \times 20 \mu$ in dimensions. The walls are smooth, with the exception of a single faint longitudinal suture that is seen on the concave side of better-preserved spores. Judging from the relative dimensions of the spores and sporangial cavities, it appears that several thousands of spores were produced in each sporangium. Figures 13 and 14 illustrate the bean-like shape of the spores and the abundance in which they were produced. Tetrads have not been observed.

Cyathotrachus altissimus differs in several ways from the two previously described species. In general proportions it corresponds rather closely with the type species, *C. altus*, but differs sufficiently in size, number of sporangia, and spore characters to warrant recognition as a separate species; likewise the differences from *C. bulbaceus* are equally significant. The more important characters of the three species are presented in the following table:

	<i>C. altus</i> Watson	<i>C. bulbaceus</i> Graham	<i>C. altissimus</i> Mamay
Sporangial dimensions	.20 × .70 mm.	.30-.35 × .65 mm.	.20-.45 × 1.50-1.80 mm.
Number of sporangia per synangium	4-7	4-6	5-9
Spores	Ovoid, $12.5 \times 15 \mu$	Round, 18μ in diameter	Bilateral, $12 \times 20 \mu$

In reference to the proportionately greater height of the synangium than that of the type species, the specific name *altissimus* is proposed and the following diagnosis offered:

Specific Diagnosis: Synangia containing 5-9 sporangia; central column extending approximately half the length of the synangium. Sporangia 1.50-1.80 by .20-.45 mm. Dehiscence by a longitudinal cleft along the innermost sporangial wall. Spores monolete, bilateral, measuring approximately $12 \times 20 \mu$; spore walls smooth, with a single longitudinal suture along the concave surface.

Age: Des Moines Series of the Pennsylvanian.

Locality: Urbandale Mine, Iowa.

Type Slides: #1687-1693.

DISCUSSION

The genus *Cyathotrachus* was considered remarkable by its discoverer from the standpoint of its striking similarity to the fructification of the living marattiaceous genus *Christensenia*. This similarity has been pointed out by other authors; the chief difference between the two fructifications lies in the mode of dehiscence, which occurs by means of apical pores in the latter. Notwithstanding its gross similarity to the living genus, Watson was reluctant to assign conclusively his discovery to the Marattiaceae for the reason which he thus expressed:

I think that two years ago no one would have hesitated to say that it belonged to the Marattiaceae. Now, however, in view of Mr. Kidston's discovery that *Crossotheca*, formerly considered to be Marattiaceous, is really the male fructification of *Lyginodendron*, whose female fructification is, of course, the seed *Lagenostoma*, it seems safer to regard it as of uncertain position, although belonging to either the Ferns or Cycadofilices, and I think most probably to the Ferns. For this reason I have put the word "Fern" in inverted commas in the title.

Although specimens referable to this genus have not been found in numbers sufficient to attract much attention,¹³ other authors (Hirmer, 1927; Scott, 1920; Seward, 1910; Arnold, 1947) have remarked on its close similarity to the genus *Ptychocarpus*. The similarity may be noted by a comparison of figs. 11 and 13, the former being a reproduction of Renault's original illustration of *P. unitus* Brongniart. If the central column were removed from the latter, the two fructifications would indeed be morphologically identical; furthermore, discounting the presence of a vascular strand in the central column and the fact that the spores are still contained within the sporangia, Renault's figure might find a favorable comparison with the specimen shown in fig. 15. As a pertinent opinion, we quote Scott (1920), who wrote: "The fructification of *Ptychocarpus unitus* is, however, a good example of a typical Marattiaceous synangium, and affords strong evidence as to the affinities of the plant."

Considering the undeniable morphological similarities between the two genera, it seems that the opinion expressed above should apply to *Cyathotrachus* as well as *Ptychocarpus*. Indeed, it appears that the bulk of the evidence weighs in favor of a marattiaceous affinity for *Cyathotrachus*. Further pertinent discussion will be presented in succeeding pages.

SCOLECOPTERIS Zenker, *Linnaea* 11:509-512. 1837.

This fructification genus was based upon silicified material from the Lower Permian of Saxony, the type species being *S. elegans*. Although the scope of Zenker's original descriptions was somewhat hampered by the poor quality of preparations available to workers of his time, the generic diagnosis is sufficiently complete that confusion of this fructification with other genera is not likely. The original diagnosis is as follows: "Capsulae hypophyllae non zonatae binae—quinae

¹³The only other specimens reported appeared in Darrah's (1941) treatment of the American coenopterid ferns, in which he reported "sporangia which have *Cyathotrachus* structure."

in unum glomus breviter stipitatum aggregatae, apice longitudinaliter hiantes. Indusium nullum."

The generic name literally means "worm fern" (Greek σκώληξ, worm; πτερίς, fern). The name was proposed in reference to the superficial resemblance of the numerous crowded pinnules to the segmented bodies of a host of maggots! This superficial similarity later caused Geinitz (1872) actually to interpret silicified *Scolecopteris* specimens as fossil millipedes; he named his specimens *Palaeojulus dyadicus* on this account (*Julus* being a modern millipede genus). Subsequent searches for the heads of these "worms" demonstrated the presence of attached fructifications and the errors of his interpretations.

In 1874 Strasburger made a more detailed investigation of Zenker's original material and redescribed the fructifications in a work which has since won acclaim among paleobotanists. This paper includes a critical comparison of the fructifications with those of other ferns and indicates his acceptance of the marattiaceous affinity of *Scolecopteris*.

Grand'Eury (1877) published very brief accounts of two additional species, *S. subelegans* and *S. ripageriensis*, from the Carboniferous of France. Although he attributed an "indusial" structure to *S. subelegans*, its presence is by no means clearly indicated. Furthermore, the two illustrations, which appear in natural size and a magnification of only two diameters, respectively, hardly present a basis for satisfactory comparisons of these fructifications with other species of *Scolecopteris*.

Several years later Renault (1883) described the fructifications of *Pecoopteris polymorpha* under the name *Scolecopteris polymorpha*. His well-known drawing of this species, which appears in almost every text-book of paleobotany, shows the synangia arranged in a single series on either side of the pinnule midrib. They are sessile, and are composed of four sporangia each, fused at their inner surfaces to a central column which extends about a third of the distance from the base. The sporangia have long, bristle-like apices. In spite of the sessile attachment of the fructifications and the central column, Renault considered it to be within the generic limits of *Scolecopteris*. This point met with disagreement in 1890 when Schimper removed the fructification genus from *Scolecopteris* and created the new genus *Acitbeca* in recognition of the generic significance of the difference between sessile and stalked synangia. Kidston (1925) concurred with Schimper's views.

Scolecopteris was assigned to the suborder Asterotheceae of the Marattiales by Stur, in 1883. The suborder was segregated to include fructifications in which the sporangia are stellately arranged; its original inclusions were the genera *Scolecopteris* Zenker, *Diplazites* Goepfert (*Ptychocarpus* Weiss), *Sturiella* Weiss (*Renaultia* Stur), and *Asterotheca* Presl. The asterothecous affinities of the two additional genera, *Acitbeca* Schimper and *Cyatbotrachus* Watson, which were not known at the time of Stur's publication, were pointed out by Graham (1934).

The first American addition to the genus *Scolecopteris* was made in 1926 when Hoskins recognized a new species, *S. minor*, from the Pennsylvanian of Illinois.

As evident from the specific name, this species is distinctive in its relatively small size.

In 1932 Scott described an additional species, *S. Oliveri*, based upon silicified specimens from the Permo-Carboniferous of Autun, France. This was followed in 1933 by a paper in collaboration with Holden, in which the foliage of the species was described. The silicifications are apparently the acme of preservation, and the descriptions and illustrations are correspondingly gratifying. The species is quite distinct from others, chiefly in its bilateral spores and the dimensions of the fructifications. Of exceptional interest, however, is the fact that the material was so well preserved that minute studies of such intimate details as epidermal hairs, ramenta, hydathodes, and stomata were possible.

Graham (1934) described the second American species, *S. latifolia*, from the Upper Pennsylvanian of Illinois. This fructification is distinct from ones previously described in its much larger spores (at least twice the diameter of other species known at the time of his publication) and the extremely inflexed, broad margins of the pinnules, from which the specific name was derived. In the same publication he reported specimens which he considered to belong to *S. minor* Hoskins, in spite of noticeably smaller pinnules and other differences, which he attributed to environment.

Andrews (1943) described the species *S. Radforthii* upon the basis of compressions from the McLeansboro formation in Illinois. Although the spores correspond closely in size with those of *S. latifolia* Graham, sporangial dimensions are not in close agreement, and the foliage shows no indication of the broad revolute nature of the latter species.

Following is a list in chronological sequence of the species known prior to this study.

- S. elegans* Zenker, *Linnaea* 11:509. 1837.
- S. subelegans* Grand'Eury, *Acad. Sci. Inst. France, Mem.* 24:72-73. 1877.
- S. ripageriensis* Grand'Eury, *Ibid.* 73.
- S. minor* Hoskins, *Bot. Gaz.* 82:427-436. 1926.
- S. Oliveri* Scott, *Linn. Soc. [London] Jour. Bot.* 49:1-12. 1932; *Ibid.* 309-321. 1933.
- S. latifolia* Graham, *Bot. Gaz.* 95:456-458. 1934.
- S. Radforthii* Andrews, *Mo. Bot. Gard. Ann.* 30:435-437. 1943.

During the past three years, many specimens of *Scolecopteris* fructifications have been studied, with the result that three new species and a tentative new variety are recognized. Furthermore, significant data have been added to our knowledge of *S. latifolia* Graham. The descriptions of this material are presented in the following pages, and at the conclusion of this chapter appears a chart comparing the significant characters of the various species, as far as they are known.

SCOLECOPTERIS LATIFOLIA Graham, emend. Mamay (figs. 17-23).

Numerous fructifications which are thought to be referable to *S. latifolia* have been observed in coal balls from various of the Iowa localities (chiefly Urbandale).

Faulty preservation and lack of associated foliar remains, however, render a positive identification of the fructifications impossible.

In recently collected coal balls from the Mineral, Kansas, locality it has been my good fortune to discover comparatively well-preserved fructifications, complete with foliage, whose identity as *S. latifolia* can hardly be questioned. However, in spite of the close correlation between various characters of our material and those given in Graham's descriptions and illustrations (1934), the Kansas specimens present significant differences which require careful consideration and warrant an emendation of Graham's original specific diagnosis.

The synangia predominantly contain three sporangia, but groups of four are comparatively common, while none with more than four have yet been found (fig. 18). The sporangia are attached at their bases to a common pedicel (fig. 17). No evidence of vascularization of the pedicel has been observed. Above the point of attachment with the pedicel the sporangia of a single synangium are quite free from each other, although in some instances they are so closely appressed that an illusion of a connection is created. There is no central column in the synangium as indicated by Graham.

Individual sporangia vary from .90 mm. to 1.20 mm. in length and from .39 to .34 mm. in width; the width is usually greatest near the base and decreases gradually toward the distal end, resulting in an acute sporangial apex (fig. 17). The outer, or free surfaces, of the sporangial walls are not appreciably thicker than the inner. When seen in transverse sections (fig. 18), the sporangia are roughly triangular, due to the close appression with adjacent ones. Dehiscence occurs, as in all other species of *Scolecopteris*, by means of a longitudinal cleft along the innermost surfaces of the sporangia.

The spore contents of the Kansas material leave much to be desired from the standpoint of preservation. Although the majority of the sporangia are nearly filled with spores, the spores are mostly collapsed or fragmentary and were apparently preserved prior to maturity, judging from the great variability in their sizes. The spores are trilete, the better preserved ones up to 35 μ in diameter. The spore walls are without any distinctive sculpturing, but faint triradiate markings have been seen in a few specimens (fig. 20).

The pinnules are arranged alternately upon the penultimate midrib, and when seen in sections transverse to the midrib have margins which are so inflexed that they nearly form a closed chamber or cylinder (fig. 17). Measured at the "shoulders," the pinnules average 2 mm. in width. This does not, however, embrace the entire width, for if the inflexed margins were flattened out the width would then approach 7 mm. Figure 17 illustrates this aspect of the pinnules very well. Here are shown two pinnules, each bearing two fructifications which are nearly enclosed by the foliar margins. The short pedicel may be seen attaching one of the synangia to the pinnule at the right. The upper surface of the pinnule is composed of an epidermal layer with a relatively thick hypodermis, the two being indistinguishable from each other. The cells of this region are filled with a dense

black substance. The lower epidermis is a very thin layer, probably a single cell thick. Between the upper epidermis and the lower the tissues are not preserved. The midrib is relatively small, and the vascular tissue is not preserved. (The midrib of the penultimate pinnule, however, has been seen to contain a u-shaped vascular strand with the open ends oriented adaxially.) Slightly below the "shoulders" of the pinnule the dense tissues of the upper and lower surfaces merge into a single tissue which composes one-third of either side of the lamina.

As seen when sectioned in the plane parallel to the lamina proper, the pinnules average 3.80 mm. in length and display the typical pectopterid outline (figs. 19 and 23). In fig. 23, the section has intercepted several of the unbranched lateral veins. The several synangia, which are sectioned very near their proximal ends, are seen to be inserted directly below the lateral veins in a single series on either side of the midrib. Figure 18, showing a specimen sectioned in a plane somewhat lower than that in fig. 23, illustrates the epidermis and hypodermis with their dense contents. Here we see eleven fructifications sectioned transversely; of these, seven contain only three sporangia each. Proceeding further downward in this series, it soon becomes apparent that we are dealing with a type of pinnule which is unique for the genus *Scolecopteris*. As the upper and lower epidermal layers merge to form the single homogeneous tissue described above and illustrated in fig. 17, this tissue becomes dissected, resulting in an *incised margin* to the pinnule. This is illustrated in fig. 19. Here the essentially pectopterid outline of the pinnule is preserved, but the margin is seen to be composed of not a continuous line of tissue, but of a series of small crescent-shaped segments averaging .50 mm. in length and .15 mm. in width, with the convex surfaces directed toward the midrib of the pinnule. In this figure, the outline of one pinnule is seen extending away from the rachis, with segments of the margins of two adjacent pinnules also present. The discreteness of the marginal lobes is best shown in fig. 21. The lamina proper, with fragments of several longitudinally sectioned fructifications attached, is seen in the upper portion of the illustration. At the lower portion appear the several marginal lobes of the pinnule. They are well-defined, separate bodies with dense cellular contents corresponding exactly to those seen in figs. 17, 18, and 19. Another conspicuous feature are the multicellular hairs attaining lengths of .50 mm., which arise from both the dorsal and ventral surfaces of the marginal lobes. Figure 22, showing a single enlarged lobe (sectioned transversely), illustrates especially well the dense cellular contents and the multicellular hairs.

By serial sections of the Kansas specimens, the following facts pertinent to *S. latifolia* have been established:

1. The lateral veins of the pinnule extend only approximately as far as the "shoulders" of the pinnule. Beyond this point they are indistinguishable, and beginning at approximately the point where they disappear, the lamina becomes dissected, the number of resultant marginal lobes usually corresponding to the number of veins. The margins of the lobes fall in the area between the veins.

2. The fructifications are inserted singly, below and near the ends of the veins; they are accordingly situated very close to the bases of the marginal lobes.

From the above information inferences of phylogenetic interest may be made which will be taken up in detail later in this paper.

In several respects the Kansas specimens correspond sufficiently with the type description that their identity with *S. latifolia* is obvious. They concur exactly in the dimensions of the fructifications, numbers of sporangia in the synangia, and in the shape and total width of the pinnules, as seen in transverse sections. A completely satisfactory comparison of the spores is not possible, but they are alike in having triradiate markings and smooth exines. Furthermore, the measurements of the spores of our material agree with Graham's specifications.

Graham described a central column in the synangium. This I attribute to a misinterpretation on his part. Such a structure, although shown in his line drawing (fig. 7 of his paper), is not apparent in the photograph which appears in his figure 27, or in his original slides.¹⁴ In his illustration and the Kansas specimens the closely appressed walls of adjacent sporangia superficially seem to be fused organically. Minute examination of the Kansas specimens has invariably proved that this is not the case, however. If a central column were present, the fructification would indeed be beyond the limits of *Scolecopteris* and would represent a fructification intermediate between the genera *Scolecopteris* and *Acitbeca*.

The dissected margin of the pinnule was not mentioned by Graham. This feature is not clearly seen in Graham's slides due to inferior preservation and absence of a section comparable to that shown in fig. 19. While it is not my intent to confuse the nomenclature of the genus, it seems that the results of this study necessitate an emendation of Graham's concept of *S. latifolia*, with particular reference to the central column and the margination of the pinnules.

Emended Specific Diagnosis: Synangia consisting of usually 3, sometimes 4, sporangia. Sporangia with acute apices and ranging from .90 to 1.2 mm. in length and from .34 to .39 mm. in width, attached basally to a short synangial pedicel, but free above; outer surfaces of walls not appreciably thicker than the inner; dehiscence by means of a longitudinal cleft along the innermost sporangial wall. Pinnules averaging 3.80 mm. in length and with total widths averaging 6.50 mm., strongly inflexed and deeply incised on the margins, with a single synangium inserted near the base of each marginal lobe and directly beneath a lateral vein; lobes averaging .50 mm. in width, with multicellular hairs borne on both surfaces. Spores spherical, to 35 μ in diameter, with trilete scars and otherwise smooth exines.

Age: Fleming coal, Cherokee shale.

Locality: Mineral, Kansas.

Type Slides: #1694-1697.

¹⁴Graham's type slides of *S. latifolia* were made available for this study through the kindness of Dr. R. M. Kosanke, of the Illinois State Geological Survey.

SCOLECopteris iowensis, sp. nov. (figs. 24–28).

Several small Urbandale coal ball slabs (WCB 511, 515, 517, 518) were found to contain an abundance of these fructifications, in many cases attached to the pinnules. The color and texture of the slabs WCB 511, 515, and 517 indicate that they probably were cut from the same coal ball, but this cannot be verified since they were sent to this laboratory already sawed.

The synangia consist of four, five, or most commonly six, elongate sporangia. They are arranged circularly and are attached at their bases to a common pedicel. The fructifications are inserted in a single or sometimes double series on each side of the pinnule midrib. The synangia average about 1 mm. in length (including the pedicel), and about .90 mm. in diameter, this dimension being dependent upon the extent to which the sporangia have spread radially. The individual sporangia average about .90 mm. in length and .33 mm. in width, with the greatest diameter usually being very near the base. Although attached at their bases to a common pedicel, the sporangia are separated throughout their entire lengths. In longitudinal section (fig. 27), they are seen to taper toward their distal ends, terminating in bluntly acute apices. The sporangial cavity, however, is roughly ovoid in longitudinal section, the sporangial apex being formed by the elongate wall cells and not representing a continuation of the cavity. The cells of the sporangial walls are approximately 30 μ in diameter and 150 μ in length.

Although preservation of the cells is not altogether complete, a sharp contrast may be noted between the outer and lateral walls of the sporangium (fig. 26). The outer walls are thicker, consisting of two or three layers of cells which have thickened walls and usually contain a dense black substance; the lateral walls, on the other hand, contain only one layer of cells which lack these thickened walls and black contents. In all the specimens examined, the cells of the lateral sporangial walls are lacking the cell wall on the side facing the adjacent sporangium (fig. 26). This condition, together with the fact that the sporangia appear to be laterally flattened in transverse section, suggests that the sporangia were probably very closely appressed prior to maturity; the separation of the sporangia upon reaching maturity very likely ruptured the walls of these cells, explaining their absence in our specimens.

Dehiscence was accomplished by means of a longitudinal slit along the innermost surface of the sporangial wall (fig. 28). The majority of the sporangia shown in this section exhibit dehiscence slits and have shed their spores.

The pedicels average about .15 mm. in length and .20 mm. in width. Their component cells are of thin-walled parenchymatous nature, measuring about 30 μ in diameter and 45 μ in length (fig. 27). There is no evidence of vascularization of the pedicel.

The spores constitute the most distinctive single feature of this fructification. In size they exceed those of all other species of *Scolecopteris*, attaining diameters of 80 μ , but averaging about 65 μ . Distinct triradiate markings and delicate reticula-

tions of the exine are present (fig. 25). The spore output was relatively small, probably not exceeding 100 per sporangium.

The pinnules have strongly inflexed margins. Normally they average about 3.50 mm. in width and 7 mm. in length, but if the inflexed margins were to be flattened out the width would be increased to about 5 mm. The structure of the pinnule is fairly well known. Figure 24 shows it to possess a strong midvein containing a terete vascular strand surrounded by large thin-walled cells, probably parenchymatous. A well-developed palisade layer is present. The upper epidermis is heavily cuticularized; the lower epidermis is also, but to a lesser extent. The mesophyll tissue lying between the point of insertion of the synangia and the margin of the pinnule consists of flat plate-like cells whose greater axes parallel the plane of the pinnule surface.

The specimen represented in fig. 24 indicates that the synangia were ordinarily borne in a single series on each side of the midvein. However, instances of departure from that condition have also been noted. Figure 28 shows a section taken through the midvein of a pinnule in a plane parallel to the plane of the lamina. Here is shown a lateral vein departing from the midrib, with two distinct rows of synangia lying parallel to the midvein. These two rows of synangia might be interpreted as belonging to two separate adjacent pinnules, but thorough investigation of this and other comparable specimens reveals that the synangia of one row are much too closely appressed with those of the other to accommodate the two inflexed pinnule margins which otherwise would have occupied the position between rows. This would indicate, then, that a single series of synangia on each side of the midvein was not always the case, some of the pinnules apparently having borne two rows of fructifications on each side.

In consideration of the spores alone, this fructification appears to be a distinct species of *Scolecopteris*. Spores of this species are seen to reach diameters of 80 μ , while those of all other species are much smaller, with the exception of *S. latifolia* and *S. major* (description on following pages). In *S. latifolia* they are known to attain a maximum diameter of 35 μ ; furthermore, the predominance of trilocular synangia, the sporangial dimensions, and unthickened outer sporangial walls of *S. latifolia* are in striking contrast to the usually 6-locular synangia, smaller sporangia and unequally thickened sporangial walls of *S. iowensis*. The specific distinctions between *S. iowensis* and *S. major* (discussed below) leave no alternative but to recognize this fructification as a new species. The name *S. iowensis* is proposed with reference to the type locality, and the specific characters are summarized in the following diagnosis:

Specific Diagnosis: Synangia borne in single or double series on each side of midvein and consisting of 4, 5, or, most commonly 6, sporangia. Sporangia free laterally, attached basally to a common pedicel, averaging approximately .35 mm. by .90 mm.; outer surfaces of walls thickened, inner surfaces thin; dehiscence by a longitudinal cleft along the innermost surface of the sporangial wall. Spores round, 65–80 μ in diameter, with triradiate scars and reticulate exines. Pinnules

averaging 7 mm. in length, normally about 3.5 mm. wide, but 5 mm. wide if unrolled.

Age: Des Moines Series of the Pennsylvanian.

Locality: Urbandale Mine, Iowa.

Type Slides: #1698-1702.

SCOLEOPTERIS MINOR Hoskins, var. *parvifolia*, var. nov. (figs. 29-33).

This extremely small fructification with its proportionately small supporting pinnules has proven to be the most abundant and widely distributed form of *Scoleopteris*. Its presence was first noted in coal balls 431 and 445, from the Urbandale Mine in Iowa, and it is chiefly on this material that the following description is based. Since the beginning of this study, however, petrifications from several other localities have been collected and sawed, and fructifications which correspond exactly with the original material have been found in coal balls from Lynnville, Ind., Berryville, Ill., Mineral, Kans., and in one tiny fragment from Shore, Lancashire, England.

An outstanding specimen consisting of the greater portion of an ultimate rachis and several attached pinnules was found in WCB 431. Although the original saw-cut sectioned the specimen slightly obliquely to the plane of the lamina, it clearly illustrates the nature of the pinnules and their fructifications.

The synangia usually contain only four sporangia, but groups of five are not uncommon and one synangium with six was found. The synangia average about .70 mm. in diameter and .65 mm. in length, including the pedicel. They are always arranged in a single series on each side of the midvein, on the dorsal surface of the pinnule. The individual sporangia are ovoid in longitudinal section, averaging from .56 to .60 mm. in length and about .35 mm. in diameter. In longitudinal section (fig. 33) the sporangial apices are seen to be more blunt than those of *S. iowensis*. Here again, the apex is formed by elongate wall cells and does not represent a continuation of the sporangial cavity. The sporangia are grouped about the common pedicel, which in this species superficially resembles a very short central column, due to the slightly oblique basal attachment of the sporangia. Basally the sporangia are closely appressed to each other (not organically fused, however); for the greater part of their lengths the lateral walls are entirely free from each other.

The outer sporangial walls are thickened, usually entailing two or more layers of cells with very heavy walls. The inner walls contain only a single layer of cells whose walls are not thickened as those of the outer wall cells. Dehiscence was accomplished by means of a longitudinal cleft along the innermost surface of the sporangial wall. The transverse aspect of dehiscent sporangia is shown in fig. 31.

The pinnules of this species are much smaller than those of other species. They seldom exceed 4 mm. in length, averaging about 3 mm.; width averages about 1.75 mm. The margins are strongly inflexed, however, and if they were flattened out the width would be increased to about 2.50 mm. The nature of the pinnules is

shown in fig. 32. This section has been cut through the lamina on one side of the midrib and through the attached synangia on the other side. The strong ultimate rachis may be seen with the pinnule midvein departing from it. Lateral veins are seen departing from the pinnule midvein. There are five synangia and five lateral veins in evidence, their relative positions indicating that the fructifications are borne directly beneath the veinlets. There is no evidence of incision of the margins. Figure 29 is a transverse section of a pinnule, further illustrating the strongly inflexed condition of the margins. Also shown is a strong midvein, although faulty preservation precludes a detailed study of the vascular tissue. Palisade tissue seems to be lacking, and the epidermal layers show no apparent cuticularization. The uniseriate insertion of the fructifications is shown in fig. 32.

The spores are badly crushed in the majority of the specimens. There is, however, a triradiate scar present, although the exine is without any additional markings. The spores are spherical, averaging approximately $15\ \mu$ in diameter (fig. 30).

Spore and sporangial dimensions distinguish this fructification from *S. latifolia*, *S. major*, *S. elegans*, and *S. iowensis*, while the morphology of the spores serves in itself to separate it from *S. incisifolia* (description to follow) and *S. Oliveri*. Had this study been limited to inspections of only a few specimens, they might have been referred to *S. minor* because of the strong resemblance. However, in view of the constancy of the cited dimensions in numerous specimens from several widely separated localities in America and one in England, the smaller sporangia and pinnules appear to constitute a reliable basis for recognizing this fructification as a small varietal segregate of *S. minor*. The characters of *S. minor* var. *parvifolia* are summarized in the following diagnosis:¹⁵

Varietal Diagnosis: Synangia borne in a single series on each side of the midrib, and consisting of 4, sometimes 5, sporangia. Sporangia ovate, with blunt apices, averaging approximately .58 mm. in length, .35 mm. in width, closely appressed at the bases, but entirely separate for the greater part of their lengths; outer surfaces of walls thickened, inner surfaces thin; dehiscence by means of a longitudinal cleft along the innermost surface of the sporangial wall. Pinnules with strongly inflexed margins, averaging 3 mm. in length, normally about 1.75 mm. in width but 2.60 mm. if unrolled. Spores round, averaging $15\ \mu$ in diameter; walls with triradiate scars and otherwise smooth exines.

Age: Des Moines Series of the Pennsylvanian; the Great Coal Ball Horizon.

Localities: Urbandale Mine, Iowa; Berryville, Ill.; Lynnville, Ind.; Mineral, Kans.; Shore, Lancashire, England.

Type Slides: #1703-1708.

¹⁵Graham (1934) described fructifications which correspond exactly with *S. minor* var. *parvifolia* in every aspect. He felt, however, that the size factor was one which could have been induced by environment and referred the specimens to *S. minor*. The constancy of the small size of this variety having been demonstrated by its widespread distribution, it seems probable that the specimens he described should be referred to *S. minor* var. *parvifolia*.

SCOLECopteris *incisifolia*, sp. nov. (text-fig. 1; figs. 34–41).

Several isolated fragments of this fructification, including three nearly complete supporting pinnules, were found in WCB 431, from the Urbandale Mine. While these specimens represent various stages of maturity and accordingly display greater variation of size, it was possible to correlate them by comparisons of the spores and the oddly incised foliage.

In one specimen in which the pinnule is sectioned at right angles to the plane of the lamina and parallel to the midrib (fig. 34), several synangia are seen sectioned transversely. These were apparently preserved prior to spore formation, as neither spores nor lines of dehiscence are noticeable. The extreme thickness of the outer walls of the sporangia is striking as compared to the thin inner walls. Of the four synangia shown here, three are trilocular, the fourth quadrilocular. An inspection of all the specimens available shows the quadrilocular synangia to be slightly more numerous than the trilocular, while synangia with more than four sporangia have not been observed.

In mature fructifications (fig. 41) the sporangia are intimately appressed to each other, with the result that the lateral sporangial walls are flattened while the outer walls are rounded. The inner, or lateral, walls of the sporangia are apparently only a single cell thick; the outer composed of at least two layers of cells. The sporangia shown in this illustration display maximum diameters of about .36 mm., the entire synangium not exceeding .80 mm. in diameter. Although this specimen does not illustrate dehiscence, others have shown it to occur by a longitudinal cleft along the innermost portion of the wall of each sporangium.

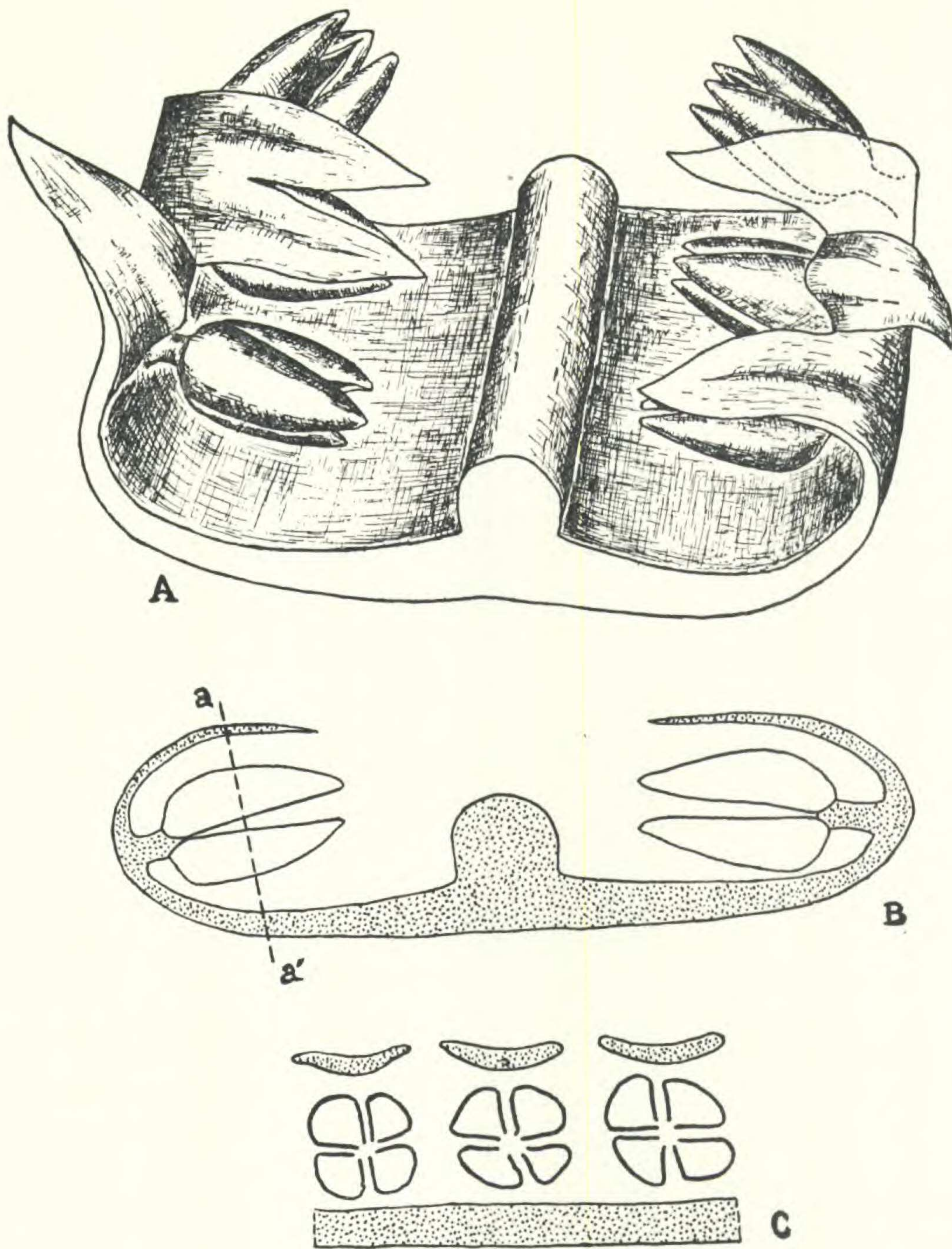
Figure 35 illustrates two immature synangia, sectioned longitudinally, from the same pinnule on which the fructifications shown in fig. 34 were borne. The foliar tissue is seen at the top of the figure and the synangia are attached to it by stout pedicels. The outstanding feature of these pedicels lies in their possession of vascular strands, each consisting of several small tracheidal elements measuring approximately 17–22 μ in inside diameter. These strands originate from the lateral veins of the pinnule, and are the only instances in which vascularization of synangial pedicels has been observed during this investigation. The pedicels shown here are about .22 mm. wide and .30 mm. long. The sporangia, which measure about .45 mm. in length and .17 mm. in width, are attached to the pedicels only by their basalmost portions.

A more mature synangium is shown in fig. 40, in which three sporangia are seen sectioned longitudinally and slightly obliquely. Their shape is roughly ovoid, with no appreciable tapering of the distal end (other specimens, however, show the sporangial apices to be typically more acute). Although the inner walls of the sporangia are closely appressed, this does not represent actual organic fusion, as observations of other specimens have proven the sporangia to be entirely free from each other throughout their lengths. The sporangia of this synangium are .45 mm. in length and .20 mm. in width. Others with lengths reaching .75 mm. have been seen, however.

The spores (fig. 39) are small, reaching $22\ \mu$ in length and $14\ \mu$ in width. They are of the monolete, bilateral type. The two spores shown here are taken from one of the synangia shown in fig. 41. The spore walls are entirely devoid of tetrad scars or other markings of the exine, and their most conspicuous feature lies in their thickness, most clearly shown in the spore at the left. The spores within a single sporangium vary in length from 18 to $22\ \mu$, and the pronounced thickness of the spore walls usually occurs in only the largest spores, which are interpreted as the most mature.

The major point of interest concerning *S. incisifolia* lies in the supporting pinnules (figs. 37 and 38). Figure 37 shows a pinnule sectioned parallel to the plane of the lamina but slightly beneath it, with the result that only the inflexed marginal portions appear. Since the color contrast between the actual specimen and the surrounding matrix was not great enough to allow for satisfactory photographic reproduction, the accompanying line drawing is offered (fig. 38). This pinnule is 5 mm. long and nearly 2 mm. wide. A portion of the midrib is seen extending proximally for some distance from the distal end. That the margins of the pinnule are strongly inflexed is shown by the fact that the margin at the upper portion of the photograph appears as a continuous line of tissue connecting both ends of the pinnule. Of particular interest here is the undulate *inner* surface of this margin, the outer surface appearing nearly smooth. This results in alternating thick and relatively thin portions of the margin. These are, in fact, the lateral veins, as each thickened portion is seen under high magnification to contain a very small vascular bundle. At point *a*, a single synangium is seen lying in essentially the same plane as the lamina proper. Proceeding now to the opposite margin (lower portion of the illustration), we see that the constrictions of the tissues lying between the veins are further accentuated, and that the margin has become incised at about the center, with two marginal lobes appearing as discrete bodies (point *b* in the line drawing). This fructification resembles *S. latifolia* in that the supporting pinnule has an incised margin, with the fructifications borne near the bases of the lobes.

A correlative inspection of fig. 34 and figs. 37 and 38 shows that the former represents a section taken parallel to the midrib, but very close to the margin and in a plane at right angles to that of figs. 37 and 38. Thus while the synangium seen in figs. 37 and 38 is sectioned longitudinally, those in fig. 34 are transversely sectioned. Here the lamina of the pinnule appears at the upper part of the photograph. Directly beneath this lie the synangia, and below them are the marginal lobes which have been so strongly inflexed that they too are sectioned transversely. It is of importance to note here that *one lobe* lies directly opposite each fructification. These are rather sausage-shaped in transverse section, with the convex surfaces directed toward the synangia. They average $90\ \mu$ in thickness and approximately .34 mm. in width. A single lobe, sectioned transversely, is shown in fig. 36. Since sections comparable to the one seen in fig. 17 (*S. latifolia*) have not been found in this material, the length of these lobes is not known. In one instance,



Text-fig. 1. Reconstruction of *Scoleopteris incisifolia*: A shows the gross aspect of the lower surface of a portion of a fertile pinnule; B, a transverse section of the pinnule; C, a section cut through plane *a-a'* of B (this approximates the section illustrated in fig. 34).

however, a lobe has been observed nearly 1 mm. in length. These structures are further illustrated in fig. 41.

Although several specimens of *S. incisifolia* show incision of the foliage essentially like that of *S. latifolia*, the marginal lobes of *S. incisifolia* are more strongly inflexed than those of *S. latifolia*, the tips pointing almost directly toward the midrib of the pinnule. The synangia are inserted one near the base of each marginal

lobe and occupying a position directly beneath a lateral vein. Like the marginal lobes, the synangia are also pointed toward the midrib. The morphology of this fructification is presented in text-fig. 1.

From the standpoint of morphology of the pinnules, *S. incisifolia* appears to be most closely related to *S. latifolia*. However, spore morphology of the two appears sufficient to separate them as two entirely distinct species. Spores of *S. latifolia* are relatively large and trilete, while those of *S. incisifolia* are small and monoete. Furthermore, the thick hypodermal layer and hirsute indument of *S. latifolia* are absent in our species. Also, the sporangial walls of *S. latifolia* are nearly equal in thickness, while those of *S. incisifolia* are noticeably thickened on the outer surfaces.

Of the remaining known species of *Scolecopteris*, *S. Oliveri* is the only other one with monoete spores, and it differs from *S. incisifolia* in the following respects: Its pinnules, although minutely toothed, cannot begin to approach the deeply incised condition of our species; the spores of *S. Oliveri* have rugose exines, while those of *S. incisifolia* are smooth; the hirsute and ramental indument of *S. Oliveri* is lacking in our species. For these reasons, in addition to the difference in dimensions of the fructifications, we feel justified in recognizing our specimens as distinct from *S. Oliveri*.

Although the material upon which this description is based is inferior in preservation to any other described specimens of *Scolecopteris*, and the number of specimens found as yet is not great enough to provide as complete an insight into the morphology as has been realized in the study of other species, the small bilateral spores and the incised foliage comprise a combination of characters not yet known to exist in any other species. For this chief reason, these fructifications appear to constitute a distinctly new species of *Scolecopteris*. The species is named with reference to the margination of the pinnules.

Specific Diagnosis: Synangia consisting of 4, sometimes 3, sporangia reaching .75 mm. in length and .36 mm. in width; sporangia blunt to acute at the apex, attached basally to a stout synangial pedicel, but free above; outer surfaces of walls thicker than the inner; dehiscence by means of a longitudinal cleft along the innermost surface of the wall. Pinnules averaging 5 to 6 mm. in length and 2 mm. in width (exclusive of the strongly inflexed margins); margins deeply incised, with a single synangium inserted near the base of each marginal lobe and directly beneath a lateral vein; lobes averaging .34 mm. in width. Spores monoete, to 22 μ long and 14 μ wide, with thick walls and smooth exines.

Age: Des Moines Series of the Pennsylvanian.

Locality: Urbandale Mine, Iowa.

Type Slides: #1709-1712.

SCOLECOPTERIS major, sp. nov. (figs. 42-46).

This description is based upon the fructification content of a single small coal-ball slab from the Urbandale locality. Although the slab originally measured only

approximately $6 \times 6 \times 1$ cm., it was found to contain numerous fructifications which are specifically distinct from other previously described species of *Scolecoperis*, and in an excellent state of preservation. The spores, however, are for the most part poorly preserved, and recognizable foliar remains to which the fructifications might be attributed are entirely lacking.

The synangia are composed of only four sporangia, except in one case where a single synangium with five sporangia was observed. The length of the synangia reaches 3 mm. (including the pedicel). In transverse section the fructifications are roughly circular, attaining diameters of about .90 mm. In all cases, the fructifications, although apparently mature and almost devoid of spores, have maintained a close appression between adjacent sporangia.

The pedicel is short and broad, measuring approximately $.35 \times .60$ mm. in the specimens in which this portion was still intact (fig. 44). It is possible, however, that the length may have been greater, since the actual attachment to foliar tissue has not been observed. The pedicel is not known to contain vascular elements.

Individual sporangia are remarkable for their extreme length. They average more than 2 mm. long, and one specimen has been found which measures 2.9 mm. long. In transverse section they appear much as the four equal segments of a circle, with the two lateral walls of each sporangium creating an angle of approximately 90 degrees. The width of the sporangia is greatest near the proximal ends, reaching .60 mm.; it gently decreases toward the distal ends, resulting in very acute apices (figs. 43 and 44). The outer walls of the sporangium are at least two cells thick, the thickness increasing toward the distal ends. The lateral or inner walls are composed of only one layer of cells, elongate in the direction of the long axes of the sporangia. The cells of the inner sporangial walls have lost their walls on the surfaces facing adjacent sporangia. In this respect the synangia, as seen in transverse section, resembles *S. iowensis* except for the number of sporangia contained. The transverse aspect of the fructifications is illustrated in fig. 42. Here the longitudinal slits of dehiscence may be noted as openings at the innermost portions of the sporangial walls (i.e., at the right angle created by the two lateral walls).

Multicellular hairs reaching 300μ in length are found on the outer sporangial walls. They are most thickly aggregated at the apices of the sporangia, their number decreasing gradually toward the bases. In fig. 46 two such hairs are seen in high magnification.

The majority of our specimens were preserved after the spores had already been shed. However, several sporangia with portions of their spore masses intact have been found. In general, the spores are round and large for this genus, the diameters ranging from 45 to 55μ . The exine is characterized by a rather coarse reticulate sculpturing, and triradiate ridges are present in the better-preserved specimens (fig. 45).

COMPARISON OF THE VARIOUS SPECIES OF *SCOLEOPTERIS*

	Average dimensions of sporangia	Number of sporangia per synangium	Nature of sporangial walls	Dimensions of pinnules	Pinnule margins	Arrangement of synangia	Spore dimensions, sculpturing
<i>S. elegans</i> Zenker	.40 × .90 mm.	Usually 5	Thickened outer surfaces; inner surfaces thin	3.50-4.00 mm. long; 1.50-1.70 mm. wide	Entire	Single series on each side of midvein	10 μ diameter; triradiate scars, smooth exines
<i>S. Oliveri</i> Scott	.44 × 1.32-1.40 mm.	Usually 4, sometimes 3 or 5	Thickened outer surfaces; inner surfaces thin	6 mm. long; 2.70 mm. wide	Minutely toothed	Single series on each side of midvein	Bilateral, with greatest dimension 18 μ; exine rugose
<i>S. latifolia</i> Graham	.34-.39 × .90-1.20 mm.	3 or 4	No thickening of outer surface	3.80 mm. long; 7 mm. wide if unrolled	Deeply incised	Single series on each side of midvein	35 μ diameter; triradiate scars, smooth exines
<i>S. Radfortbii</i> Andrews	.25 × .70 mm.	3 or 4	?	3 mm. long; 2 mm. wide	Entire	Single series on each side of midvein	32 μ diameter; triradiate scars, smooth exines
<i>S. minor</i> Hoskins	.28 × .70 mm.	Usually 4, sometimes 5, rarely 6	Thickened outer surfaces; inner surfaces thin	6-7 mm. long; 3.30 mm. wide	Entire	Single series on each side of midvein	17 μ diameter; no markings
<i>S. minor</i> var. <i>parvifolia</i> Mamay	.35 × .58 mm.	Usually 4, sometimes 5, rarely 6	Thickened outer surfaces; inner surfaces thin	3 mm. long; normal width 1.75 mm.; 2.60 mm. if unrolled	Entire	Single series on each side of midvein	15 μ diameter; triradiate scars, smooth exines
<i>S. iowensis</i> Mamay	.35 × .90 mm.	4, 5, usually 6	Thickened outer surfaces; inner surfaces thin	7 mm. long; normal width 3.5 mm.; 5 mm. if unrolled	Entire	Single or double series on each side of midvein	65-80 μ diameter; triradiate scars; reticulate exines
<i>S. major</i> Mamay	.50 × 2.10-2.90 mm.	Usually 4, rarely 5	Thickened outer surfaces; inner surfaces thin	?	?	?	45-55 μ diameter; triradiate scars; irregularly reticulate exines
<i>S. incisifolia</i> Mamay	.33 × .75 mm.	3, usually 4	Thickened outer surfaces; inner surfaces thin	5-6 mm. long; 2 mm. wide (exclusive of the inflexed margins)	Deeply incised	Single series on each side of midvein	Bilateral, 22 × 14 μ; smooth exines

Although associated foliar remains are not distinguishable, these fructifications, judging from their general orientation, seem to have been preserved in their natural position. They are nearly all oriented in the same direction and very closely crowded (fig. 42). For this reason it seems safe to assume that these fructifications, like those of *S. iowensis*, were borne in more than one series on each side of the midrib of the pinnule.

A comparison of *S. major* with the other known species of *Scolecopteris* reveals several significant differences, the most notable one being the size of the sporangia. The species most closely approaching *S. major* in sporangial dimensions is the English species *S. Oliveri* Scott. However, the average difference in length of sporangia is approximately 1 millimeter. In addition, the small bilateral spores of *S. Oliveri*, in contrast to the large trilete spores of *S. major*, lend much further weight to a specific distinction between the two.

Of the remaining species of *Scolecopteris*, none approaches *S. major* in size. The sporangium is up to 1.6 mm. longer than that of any other species, which constitutes a large difference in consideration of the generally small size of the fructifications. In spore size, *S. major* seems to occupy a position intermediate between *S. latifolia* Graham and *S. iowensis*. Although the spores are somewhat smaller than those of *S. iowensis*, from the standpoint of morphology and exine sculpturing, they correspond more closely to those of that species. It seems indeed that the closest relationship of *S. major* lies with *S. iowensis*. As has been previously pointed out, single sporangia of the two species appear extremely similar as seen in transverse section. Furthermore, if the assumption that the synangia of *S. major* were borne in more than a single series on each side of the midvein should ultimately be proven to be a correct one, the relationship between the two species will be materially strengthened. However, the presence of hairs on the fructification, the almost exclusive predominance of synangia with only four component sporangia, and the great size of *S. major* serve as sufficiently distinctive characters to warrant its recognition as a separate species. The specific name *S. major* is proposed, in reference to the large size of the fructifications.

Specific Diagnosis: Synangia consisting of 4, rarely 5, sporangia basally attached to a short pedicel. Sporangia from 2.10 to 2.90 mm. long, averaging .50 mm. in width; outer walls thickened, inner walls thin; dehiscence by means of longitudinal clefts along the inner sporangial wall; multicellular hairs reaching 300 μ in length produced on outer sporangial walls. Spores round, from 45 to 55 μ in diameter, with triradiate ridges and coarsely reticulate exines.

Age: Des Moines Series of the Pennsylvanian.

Locality: Urbandale Mine, Iowa.

Type Slides: #1713-1717.

Eoangiopteris Andrewsii, gen. et sp. nov. (text-fig. 2; figs. 47-53).

The marattiaceous fructifications dealt with thus far in this paper are those which display radially symmetrical arrangement of the sporangia. The opinion expressed by various authors that this type of fructification represents the archetype in the Marattiaceae has indeed been strengthened by the results of this study. There is no apparent reason to doubt the validity of such an opinion, considering the great predominance of radial sori in the Carboniferous rocks in which the oldest known members of the Marattiaceae are found.

At this point it seems desirable to present a cursory survey of the living Marattiaceae from the standpoint of soral morphology. Of the seven living genera of this family, only one produces radial sori (*Christensenia*). All other living genera produce fructifications which display linear or bilateral symmetry. The predominance of linear sori among the living Marattiaceae, as opposed to the predominance of radial sori among the Carboniferous representatives of the family, poses the following questions: When did the linear sorus first appear on the scene? How did it evolve? It is known that the linear sorus was already well developed by Triassic times (*Danaeopsis* Heer; *Marattiopsis* Schimper), and the presence of the genera *Danaeites* Goeppert and *Parapecopteris* Grand'Eury in the European Coal Measures indicates a very early origin for this type of fructification.

In the genus *Eoangiopteris* we find a fructification with linear arrangement of the sporangia, but with certain characters strongly reminiscent of *Scolecopteris*. Whether or not it represents the actual ancestral type from which the linear sori of certain of the living marattiaceous genera were derived cannot be conclusively stated at this time. It appears to represent a step in that direction, however, and the matter will be discussed in detail in the phylogenetic section at the end of this paper.

Numerous scattered fragments of this fructification have been found in coal balls 437A, 437B, 442, 500, 501, 502, 516, 678, 679, and 680, of the Washington University collection. These coal balls are all from the Urbandale mine. While the majority of the fragments studied consist of only a single sorus, six specimens have been found which contain more or less complete fertile pinnules (WCB 437A, 442, 501, 502, 679).

Although *Eoangiopteris* lacks the predominant radial sori such as found in the fossil genera *Scolecopteris*, *Ptychocarpus*, and *Cyathotrachus*, it agrees structurally with those living marattiaceous genera whose fructifications are linear and free-sporiangiate (*Archangiopteris*, *Angiopteris*, and *Macroglossum*).

The number of sori produced by a single pinnule ranges from 12 to 18. They lie closely spaced and parallel to each other on the dorsal surface of the pinnule, extending from the midrib as far as the inflexed margin. Their linear axes create an angle of approximately 40 degrees with the midrib, the angle of divergence from the perpendicular being toward the apex of the pinnule. By serial peels of the specimen found in WCB 442, it has been established that the sori lie directly beneath and parallel to the lateral veins.

The sori are attached to the pinnule by fleshy receptacles (figs. 48, 51) composed of undifferentiated isodiametric cells averaging 75μ in diameter. Figure 51 represents a sorus sectioned through its long axis in the plane parallel to the long axes of the sporangia; here the receptacle is shown to be approximately half as deep as the length of the sporangia, with the point of attachment to the pinnule somewhat shorter than the total length of the sorus, which ranges from .90 to 1.35 mm. The sori average about .45 mm. in width. The receptacle is not vascularized.

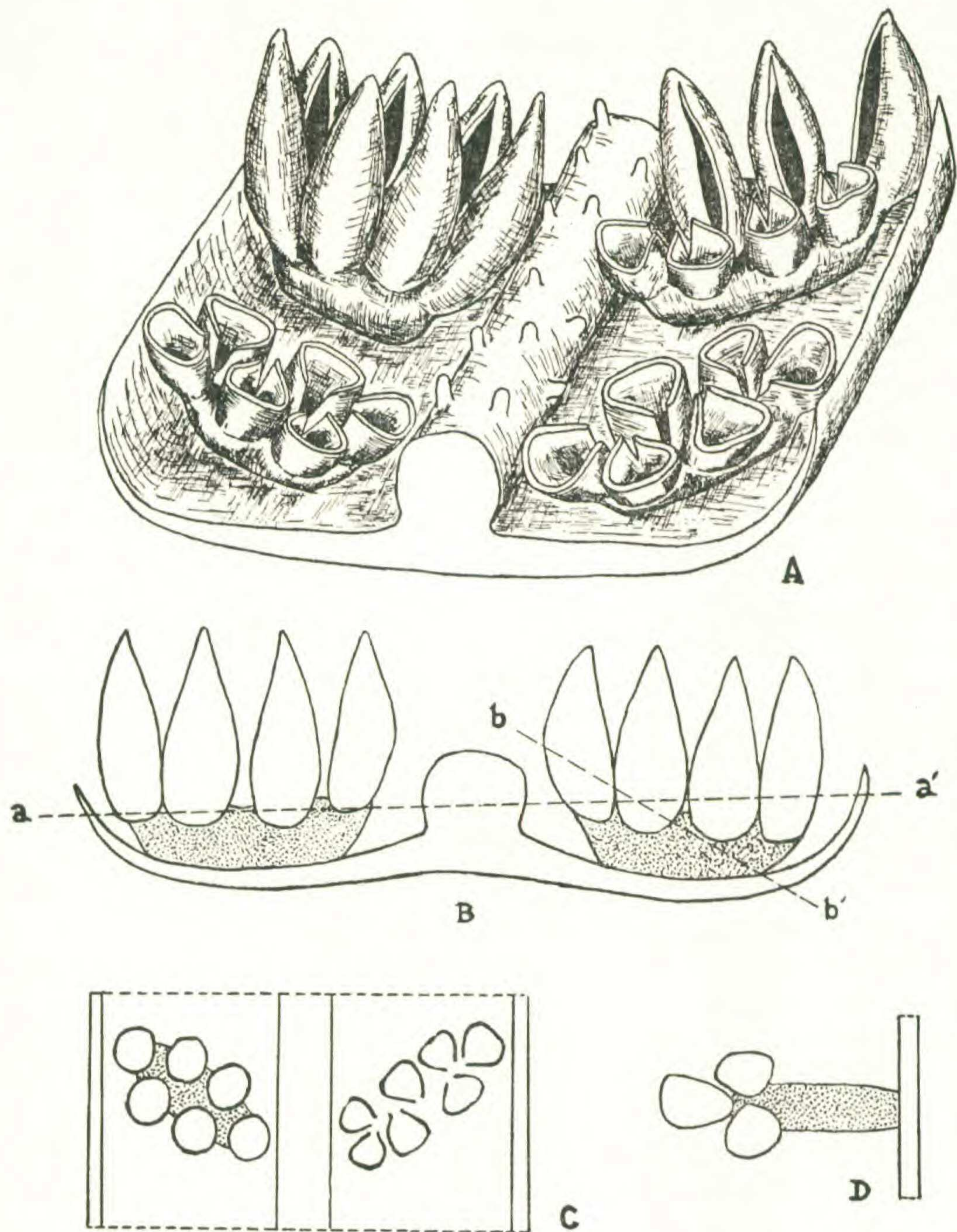
The number of sporangia in the sorus ranges from five to eight, the sori with fewest sporangia being found nearest the distal end of the pinnule. The bases of the sporangia are shallowly immersed in the tissue of the receptacle, but beyond this point of attachment there is no organic connection between adjacent sporangia. A transverse section through the basal portions of the sporangia (fig. 49) shows them to be oval and approximately .25 mm. in diameter, with the receptacular tissue distinguishable between sporangia. A section taken above the point of attachment to the receptacle (fig. 50) shows the sporangia to be roughly triangular in transverse section; in longitudinal section (fig. 51) they are elongate and pyriform, with the greatest width near the point of attachment to the receptacle. In length the sporangia range from .75 to .90 mm., those in the center of the sorus being slightly longer than those at either end. The sporangia of a single sorus are arranged in two rows, each containing up to four sporangia. The rows are either directly opposed or slightly enmeshed in each other, much as the teeth of two gears.

Although preservation of the sporangial walls is not as complete as desirable, it is evident that they are composed of at least two layers of cells. The outermost cells are thick-walled and contain a dense black substance very similar to that observed in the corresponding tissue of *Scolecopteris iowensis*. The inner cell walls are usually thinner than the outer.

Dehiscence (fig. 50) occurs by means of a longitudinal cleft along the innermost wall of the sporangium, the opening extending from the apex of the sporangium to its point of attachment. In details of dehiscence and cellular structure of the sporangial walls the sporangia of *Eoangiopteris* are strongly reminiscent of those of *Scolecopteris iowensis*—so much so, in fact, that single isolated sporangia of the two fructifications would scarcely be distinguishable, discounting the slight discrepancy in size.

Most of the spores are badly crushed, but their salient features have been determined from a few well-preserved specimens. The spores are spherical, with quite thick walls, and range from 45μ to 60μ in diameter. The exine shows faint triradiate ridges, but its outstanding feature lies in the nature of the sculpturing. In fig. 52 the exine is seen to be marked by numerous closely spaced, roughly circular pits averaging 4μ in diameter. The spore output was apparently low, each sporangium having produced a maximum of approximately a hundred spores.

The pinnules range from 7 to 9 mm. in length and from 2.50 to 3 mm. in width. The distal ends are usually somewhat narrower than the proximal. The



Text-fig. 2. Reconstruction of *Eoangiopteris Andrewsii*: A, lower surface of a portion of a pinnule with four synangia attached, the two lower synangia having been transversely sectioned; B, transverse section through the pinnule and two synangia, receptacle shaded; C, left, a section of synangium taken through plane *a-a'* of B (approximately same sectional plane as shown in fig. 49); C, right, approximately the section shown in fig. 50; D, section through plane *b-b'* of B (approximately the same as shown in fig. 48).

margins are strongly inflexed, appearing as a more or less continuous line of tissue surrounding the fructifications when seen in sections that have been made in a plane parallel to and below that of the lamina. In the light of our present knowledge of the fossil Marattiaceae we may conclude that these pinnules represent the ultimate divisions of a several-times compound frond belonging to the *Pecopteris* group. Further evidence in support of this opinion is seen in the vascular anatomy of the specimen shown in fig. 53. This represents the midrib of a pinnule, sectioned transversely. The outermost tissue consists of large collenchyma-like cells, with a few outstandingly large ones, possibly of secretory nature, interspersed among them. The inner zone consists of several layers of smaller, thin-walled cells surrounding a horseshoe-shaped vascular strand (fig. 53a) whose open ends point adaxially. The shape of the vascular strand suggests this pinnule to be the ultimate division of a *Stipitopteris* or some closely allied psaronian petiole containing a horseshoe-shaped leaf trace.

A few multicellular hairs, ranging to .20 mm. in length, have been observed on the midrib of the pinnule (fig. 53b).

A reconstruction of *Eoangiopteris* is presented in text-fig. 2.

The linear, free-sporangiate sori of the genus *Grand'Eurya* Stur, from the Permo-Carboniferous of Autun, are quite similar to those of *Eoangiopteris*. In *Grand'Eurya*, however, there is no evidence of a receptacle, the sporangia being sessile on the pinnule. This difference presents a close parallel to the generic difference between *Scolecopteris* and *Asterotheca*.

Only two other linear marattiaceous fructifications are known which closely approximate *Eoangiopteris* in age. They are *Danaeites* Goepfert¹⁶ from the European Coal Measures, and *Parapecopteris* Grand'Eury from the Upper Carboniferous of Gard and St. Étienne. However, their sporangia are laterally fused, while those of *Eoangiopteris* are entirely free from each other. Another major difference is the mode of attachment to the lamina; in *Eoangiopteris* the sori are elevated from the surface of the lamina by a receptacle, while, at least in *Danaeites*, they are sunken within the foliar tissue. These differences correspond closely in magnitude to the generic differences between the fructifications of such living marattiaceous genera as *Danaea* and *Angiopteris*.

A survey of the remaining known linear sori found among the fossils reveals none with which *Eoangiopteris* might be considered congeneric. A superficial examination of the Permian genus *Chansitbeca* Rege (for a full account see Halle, 1927), which is known from compressions only, reveals a rather close similarity to *Eoangiopteris*, from the standpoint of general shape and distribution of the sori. *Chansitbeca*, however, has sporangia with well-defined annuli, for which reason Halle ascribes to the genus a close affinity with *Oligocarpia* rather than with any marattiaceous entity.

¹⁶The generic name implies a relationship with the modern genus *Danaea*. This implication has not met with credence, however, because of the lack of sufficiently detailed illustrations.

The Rhaetic genus *Marattiopsis* Schimper consists of linear fructifications, but here the alliance is obviously one with the modern *Marattia*, since the fructifications consist of two rows of fused sporangia, the whole structure opening much as the shell of a bivalve.

The upper Triassic fructification *Danaeopsis* Heer (also known only as compressions) consists not of fused sporangia, as might be inferred from the generic name, but of two rows of free sporangia extending from the margin to the midrib of the lamina. Discounting the great differences in size of the pinnules and numbers of sporangia in a single sorus, *Danaeopsis* resembles *Eoangiopteris* almost as closely as does the previously mentioned genus *Grand'Eurya*. The salient differences, however, are sufficiently obvious that confusion of the two genera is unlikely.

Among the living Marattiaceae with linear fructifications, the genera *Macroglossum*, *Archangiopteris*, and *Angiopteris* possess free sporangia, in which respect they resemble *Eoangiopteris*. While the fossil record is not yet sufficiently complete to allow us to draw incontestable conclusions as to phylogenetic series in the Marattiaceae, it seems reasonable to consider this fructification as an intermediate form between the Carboniferous radial sorus and the free-sporangiate linear sorus of today as typified by *Angiopteris*. For this reason the generic name *Eoangiopteris* is proposed. The generic and specific characters of *E. Andrewsii* are summarized in the following diagnoses:

Generic Diagnosis: Sori linear, consisting of several exannulate sporangia arranged in two opposed or slightly intercalated rows, and inserted by fleshy receptacles along lateral veins on dorsal surfaces of pectopterid pinnules; sporangia free from each other, with bases slightly sunken in receptacular tissue; dehiscence by longitudinal clefts along inner sporangial walls.

Specific Diagnosis: Pinnules measuring 7-9 × 2.50 to 3 mm., bearing 12 to 18 sori .90 to 1.35 mm. long, with 5 to 8 sporangia per sorus. Sporangia .75 to .90 mm. long, tapering from basal diameters of .20 to .30 mm. to bluntly acute apices; walls generally 2 cells thick. Spores round, with triradiate ridges and measuring 45-60 μ in diameter; exine with circular reticulations approximately 4 μ in diameter.

PHYLOGENETIC CONSIDERATIONS

I. THE PROBLEM: THE ORIGIN OF THE MARATTIACEAE

While the specimens described in the foregoing pages have added to the specification of known fructification genera, to a clearer understanding of the nature of previously described species, and to the Carboniferous flora of the United States, their significance is not limited to those phases of paleobotany. It is the aim of paleobotany to fill in the numerous gaps in our understanding of plant evolution. The problem of the origin of the Marattiaceae has interested me for some few years, because they seem to have appeared upon the scene very suddenly during the Upper Carboniferous, leaving but few clues as to the nature of their pro-

genitors and the processes involved in their emergence as a well-defined and highly evolved fern group.

The problems of fern phylogeny are most successfully solved through comparative studies of the fructifications. Fortunately there was an amplitude of fructification specimens available for this investigation, and through their study several important points in connection with the phylogeny of the Marattiaceae have been brought to light.

II. THE "PHYLETIC SLIDE"

Studies of the various fern groups have shown that marginal or terminal fructifications are primitive, while those occupying a superficial position are advanced. The "phyletic slide," or migration of the sorus from the marginal to the superficial position, is a phenomenon which is known to occur independently in several groups of living ferns (see Bower, Vol. I, Chap. XII); it entails series of forms which display characters intergrading between the two extremes of soral position. While such series have greatly facilitated the understanding of family relationships, their presence has injected a great measure of difficulty into the task of drawing clear-cut lines of distinction between several of the families. In fact, the net result has been an extremely involved "phyletic bush" (see Bower, Vol. III, p. 2), containing intergrading and poorly defined families, with the Polypodiaceae (representing perhaps the epitome of polyphyletic and "indefinability" when considered as a single "family") occupying the most advanced position. This does not, of course, hold true for all the fern families, for at the base of the "bush", the eusporangiate families (Ophioglossaceae and Marattiaceae) present no difficulties when the "bush" as a whole is viewed. By virtue of their massive exanulate fructifications alone these two families occupy the two basal branches of the "bush"; furthermore, they are readily separable from each other by the position of the fructifications, those of the Ophioglossaceae occupying the primitive marginal position, and those of the Marattiaceae being borne superficially as clearly circumscribed sori, usually synangial. In succeeding pages an attempt will be made to explain the derivation of the superficial position of marattiaceous sori.

III. THE FOSSIL MARATTIACEAE

Marattiaceous fructifications are abundant in American coal balls from numerous localities. The lack of comprehensive and critical studies may be attributed to their small size, and it is very likely that many interesting specimens have been overlooked on this account.

Prior to the discovery of the pteridosperms, paleobotanists treated these fossils as archaic members of the Marattiaceae. Following this important discovery, however, the undeniable likenesses between the fossil and living fructifications came to be considered of less importance than the rather vague supposed likenesses between the marattiaceous fructifications and those presumed to be pteridospermous. Many attempts have been made to link these two unrelated groups upon

insufficient evidence. Kidston (1925) expressed this viewpoint in his exhaustive work on the British Carboniferous flora:

In *Acitbeca*, individual sporangia agree so closely with the microsporangia of *Telangium*, that the affinities of *Acitbeca* seem to be Pteridospermous. If, then, this opinion as to the systematic position of *Acitbeca* Schimper be correct, I do not see on what ground *Asterotheca* Presl and *Scolecopteris* Zenk. can be excluded from the Pteridosperms.

It would therefore appear that the evidence in support of the occurrence of the Marattiaceous Ferns in Carboniferous times rests on supposition rather than on satisfactory proof. This statement may be thought too strong, but what has been learnt in regard to Pteridospermous microsporangia has undoubtedly weakened the grounds on which the belief in the existence of Carboniferous Marattiaceous Ferns was founded.

EVIDENCE RELATING TO THE MARATTIACEOUS AFFINITY OF THE FOSSIL FRUCTIFICATIONS

1. *A Comparison of Pteridospermous Microsporangiate Organs and Marattiaceous Fructifications.*—

All fructifications suspected of pteridospermous affinity resemble the marattiaceous fructifications *only* in their exannulate and sometimes synangial features (which are also found among the coenopterid fructifications, those of *Stauropteris* and *Chorionopteris* being exannulate, while those of *Corynepteris* and *Chorionopteris* are synangial). Other characters, however, if compared critically, seem to invalidate these similarities as grounds for seriously considering such forms as *Scolecopteris* and others as pteridospermous. These are:

a. Size and Complexity.—While the marattiaceous fructifications rarely attain lengths of more than two millimeters, the majority of the apparently pteridospermous male fructifications (*Dolerotheca*, *Potonia*, *Whittleseya*, etc.) are huge in comparison; there is also a corresponding difference in spore sizes. Furthermore, the marattiaceous fructifications are structurally simple compared to the extremely complex organization of the fructifications mentioned above (see Halle, 1927; Schopf, 1948).

b. Manner in which the Fructifications are Borne.—In all instances where a closer compatibility of sizes can be demonstrated (*Telangium* and *Crossotheca*), the apparently pteridospermous fructifications are borne either terminally (this holds true for the larger forms, also) on naked frond ramifications or marginally on more or less peltate receptacles which terminate the ultimate frond divisions. All the known marattiaceous fructifications, however, are borne superficially on pinnules which show no difference from the sterile ones. *There is no known instance* of a pteridospermous microsporangiate fructification being borne superficially on monomorphic foliage.

c. Associations and Anatomical Evidence.—The following intimate fructification-foilage associations are known to occur: *Crossotheca* and *Sphenopteris* (Andrews and Mamay, 1948); *Goldenbergia* and *Neuropteris*, *Whittleseya* and *Alethopteris*, *Potonia* and *Neuropteris* (Halle, 1929, 1933); *Dolerotheca* and *Alethopteris* (Schopf, 1948). There is good evidence for the pteridospermous affinity of the foliage genera mentioned above, and while association alone cannot always be held as conclusive evidence, Schopf (1948) has pointed out significant histological similarities between *Dolerotheca* fructifications and *Medullosa* stems

and petioles. On the other hand, *Pecopteris* foliage, upon which the marattiaceous fructifications are borne, is known to occur in intimate association with *Psaronius* stems. Furthermore, the u-shaped vascular strands of the pinnules upon which these fructifications are borne suggest them to be ultimate divisions of a stipitopterid psaronean petiole.

2. *A Comparison of Fructifications of the Living and Fossil Marattiaceae.*—

The following significant points of similarity are demonstrated by a comparison of the living and fossil members of this family:

a. There is a close similarity in sizes of the fossil and living fructifications and spores.

b. In both the living and fossil Marattiaceae, the fructifications are in the form of definitely circumscribed sori, either free-sporangiate or synangial, radial or linear. The similarities between *Ptychocarpus* (fossil) and *Christensenia* (living) and between *Eoangiopteris* (fossil) and *Angiopteris* (living) are much closer than any which can be demonstrated between the fossil marattiaceous sori and any supposedly pteridospermous fructifications.

c. In both the living and fossil Marattiaceae the sori are restricted to a superficial position, and the foliage is monomorphic (only in the living genus *Danaea* is there anything approaching the dimorphic condition).

d. *Psaronius* stems, which are frequently found in intimate association with fertile *Pecopteris* foliage, show a close anatomical similarity to the living marattiaceous genus *Angiopteris*, and cannot be confused with any known pteridospermous stem. Furthermore, the u-shaped trace of the psaronean petiole *Stipitopteris* is quite similar to the traces found in fertile pecopterid pinnules.

It is my opinion that the foregoing evidence, if carefully considered, should lead to the conclusion that the existence of a well-defined group in the Paleozoic, corresponding in a remarkable fashion to the living Marattiaceae, cannot be reasonably denied. Furthermore, efforts made in respect to this group should be directed toward the solution of problems bearing upon their poorly understood phylogeny rather than attempting to correlate them with the pteridosperms on slender threads of evidence.

IV. A PROPOSED EXPLANATION OF THE ORIGIN OF THE MARATTIACEAE

The following facts with reference to the fossil Marattiaceae become increasingly important:

1. The fossil fructifications are essentially identical with the living ones; evolution of the fructifications had apparently reached its peak during late Paleozoic times and then leveled off.

2. The superficial position of the sorus, considered to be the climactic evolutionary result, had been well established in the Marattiaceae by Upper Carboniferous times.

Tentatively accepting the Marattiaceae as derivatives of some branch of the coenopterids, it seems likely that various stages in the migration of the sorus to

the superficial position might be sought in the coal balls, since the two groups were contemporaneous during at least part of their respective geological histories, and fructifications of both groups are frequently found within the same petrification. In searching for intermediate forms, then, we would look for either coenopterid fructifications showing tendencies toward the marattiaceous types (massive sporangial walls, synangia, or otherwise closely circumscribed sori) and occupying a terminal or marginal position, or for marattiaceous fructifications occupying marginal or only slightly superficial positions on the lamina.

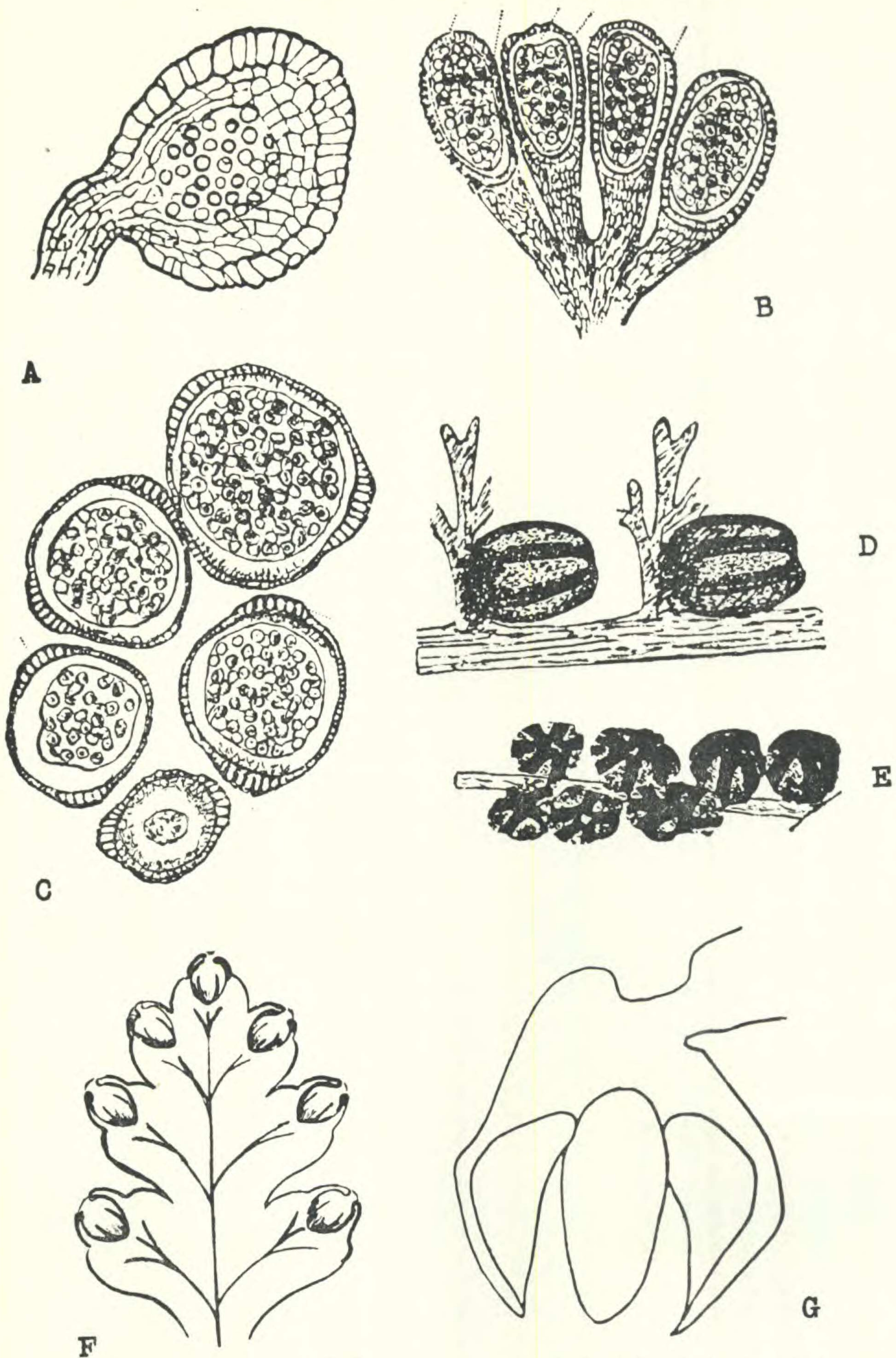
A. A REVIEW OF COENOPTERID SORAL MORPHOLOGY

In the following brief review of the outstanding aspects of some of the known coenopterid fructifications, we shall follow the sequence which Bower (Vol. II, p. 39) suggests to represent a line of soral evolution among the coenopterids.

Beginning with the simplest type of fructification, that of *Stauropteris* (see text-fig. 3A), we see that the sporangia are massive-walled, exannulate structures which are borne singly, each occupying the terminal position upon an ultimate ramification of the plant, much in the same manner as the sporangia of *Rhynia*. Continuing with the series, the sporangia of the fructification *Etapteris* (B and C) appear singly in the terminal position, but are arranged into rather lax tassel-like groups, each group suggesting a derivation from a *Stauropteris*-like progenitor by the aggregation of several individual sporangia. Although this concept is somewhat confused by the appearance of a rather well-developed annulus in *Etapteris*, the chief significance lies in the apparent tendency of the sporangia to become condensed into more intimate association with each other. A further continuation of this tendency may be seen in the genus *Corynepteris* (D and E), in which the sporangia possess annuli much like those of *Etapteris*. However, the condensation of the sporangia has been furthered to the extent that well-defined sori are present in which the sporangia are closely appressed. The sori are borne upon the margins of narrow pinnules. This is the first appearance of a lamina in this series.

The culmination of the tendencies shown in this series appears in the fructification *Chorionopteris* (F and G). Although this fructification has been reported but once, enough is known of its structure to afford the following significant facts:

1. The fructifications are massive-walled synangial groups of four sporangia each, with a continuous sheath surrounding the entire structure.
2. The fructifications are borne singly at the terminations of the lateral veins of a narrow, fleshy pinnule; the pedicels and synangial walls were originally described as "continuations of the tissues of the lateral veins." The synangia are seen to extend from the tips of the foliar lobes; they may thus be termed either *marginal* or *terminal*, depending upon whether the reference is made to the lamina or veins.



Text-fig. 3. A, *Stauropteris Oldhamia* Binney, from Bower, after Mrs. D. H. Scott (approx. $\times 50$); B, C, *Etapteris* sp., from Bower, after Renault (B, approx. $\times 10$, C, approx. $\times 20$); D, *Corynepteris Essenghi* Andrae, from Bower, after Zeiller (approx. $\times 10$); E, *Corynepteris coralloides* Gutbier, from Bower, after Zeiller (approx. $\times 5$); F, G, *Chorionopteris gleichenioides* Corda, from Hirmer, after Kubart (F, approx. $\times 9$, G, approx. $\times 20$).

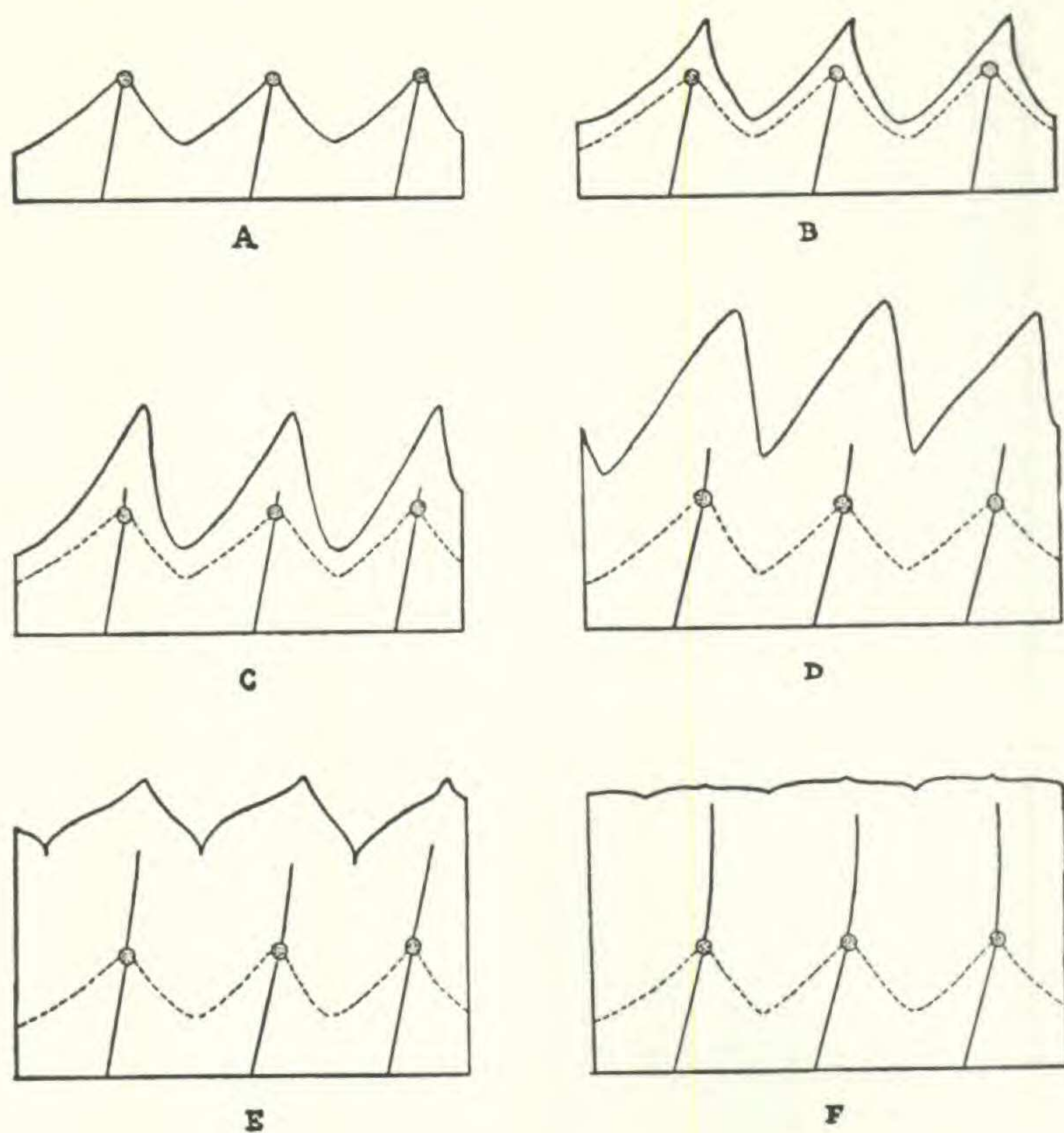
Although the fact that both annulate and exannulate sporangia are involved in the above series seems to cast doubt upon its validity as a single natural sequence, its value lies in the apparent tendency of the fructifications to become aggregated into compact groups which are ultimately borne on the margin of a distinct lamina. It appears that the genera *Stauropteris* and *Chorionopteris*, with their exannulate, thick-walled sporangia, represent the opposite extremities of one line of development within the coenopterids, which leads to the Marattiaceae. The intermediate members of this line are as yet unknown. The genus *Corynepteris*, on the other hand, seems to represent a stage in still another series involving annulate sporangia, which may have culminated in a gleicheniaceous form such as *Oligocarpia*. Information concerning the development of the lamina in these genera is totally lacking.

B. A "PHYLETIC SLIDE" SERIES

Referring back to the fructification *Chorionopteris*, its salient features seem to fulfill the qualifications for a progenitor of the Marattiaceae.¹⁷ The synangia would be easily confused with a scoleopterid fructification if their relationship with the coenopterid petiole *Anachoropteris* were not known. The sporangia of *Chorionopteris* are enclosed by a continuous synangial wall, a feature which is by no means absent in the pectopterid fructifications. It is found in the genera *Cyatbotrachus* and *Ptychocarpus*, and in young synangia of *Scolecopteris incisifolia* (fig. 34). Since the chief difference between *Scolecopteris* and *Chorionopteris*, then, lies in their relative positions on the lamina, we are faced with the problem of demonstrating stages intermediate between the marginal and superficial positions. The species *Scolecopteris incisifolia* and *S. latifolia* appear to represent such intermediate stages; the evidence points toward migration of the sorus to the superficial position in which *proliferation* of the upper tissues of the margin of a chorionopterid pinnule produced one like that upon which the two mentioned species of *Scolecopteris* were borne.

The reader is now referred to text-fig. 4, in which a series of diagrams representing marginal portions of fertile pinnules is presented. In *A* (*Chorionopteris*), the synangial points of attachment are seen at the tips of the marginal lobes of the pinnule, each one terminating a lateral vein. In *B* (hypothetical) the marginal tissues have proliferated slightly; the inter-lobal embayments of the lamina are still comparatively wide; but the synangial points of attachment are now slightly superficial. In *C* (hypothetical), the proliferation has continued, and the lateral veins have extended slightly beyond the points of attachment of the synangia. *D* represents a stage approximating the condition found in *Scolecopteris incisifolia*

¹⁷Bower (Vol. II, p. 39) states, in reference to *Chorionopteris*: "A 'phyletic slide' of the sorus to the lower surface of a widening leaf segment . . . would then give a soral state similar in structure and position to that seen in the Marattiaceae."



Text-fig. 4. Illustrating a possible "phyletic slide" series, beginning with the coenopterid fructification *Chorionopteris* and resulting in the marattiaceous fructification *Scolecopteris*. Shaded circles represent the points of insertion of the synangia; broken lines the original foliar margin shown in A.

(compare with text-fig. 1) and *Scolecopteris latifolia*. The lobes are now proportionately longer than wide, and the embayments of the lamina are quite narrow. The synangia are inserted near the bases of the marginal lobes and the ends of the lateral veins, and are now quite superficial in position. In *E* (hypothetical) the lobes have undergone lateral fusion to some extent, a process which is culminated in *F*, in which the margin of the pinnule is essentially entire. This would correspond to the condition seen in *Scolecopteris iowensis* or *S. minor*.

Such a series may also be seen in the ontogeny of various genera of the living Schizaeaceae. The young sporangia begin their development in a marginal position, to be followed by a proliferation of the upper tissues of the margin of the lamina, causing the matured sporangia to assume a superficial aspect. This may represent the ontogenetic reflection of a phylogenetic series such as diagrammed in text-fig. 4, but involving annulate sporangia.

As seen in fig. 17 (*Scolecopteris latifolia*), the tissues composing the long, narrow marginal lobes seem quite definitely to be direct continuations of the upper epidermal and hypodermal tissues which are characterized by their dense black

cellular contents. This aspect may be best seen in fig. 22, a transverse section of a single lobe. Although the lobes are quite discrete bodies, they are very closely crowded, and it appears that their lateral fusion to form a continuous-margined lamina such as that upon which *S. iowensis* was borne, would present little evolutionary difficulty. Thus the genus *Scolecopteris* is seen to contain forms (*S. latifolia* and *S. incisifolia*) which are intermediate between the marginal and superficial conditions.

There yet remains one puzzling aspect of this hypothesis. Among the coenopterid fragments present in American coal balls, the petiole *Anachoropteris*, which is known to have borne *Chorionopteris* fructifications, is found in numbers exceeded only by fragments of *Botryopteris*. However, fructifications which compare in detail with the original descriptions and illustrations of *Chorionopteris* still remain to be discovered in our petrifications. Furthermore, although the stems upon which *Anachoropteris* petioles were borne are still unknown, the comparatively large size of the petioles suggests an origin from a stem of such magnitude that it could hardly escape notice. What then are we to deduce from the total absence of stems and fructifications in floras so rich in petiolar fragments? The following suggestions are offered for consideration:

1. The close fundamental resemblances between *Chorionopteris* and various of the scolecopterid species suggests that they compose an evolutionary complex of intergrading forms, and any or all of the intermediate forms presented in the series shown in text-fig. 4 might be sought within either genus. The generic distinction would then depend upon the vascular anatomy of the supporting petiole.

2. *Anachoropteris* petioles, when seen in transverse section, display vascular strands with similar structure to those of the psaronian petiole *Stipitopteris*, with the exception of the position of the protoxylems. They may in all likelihood be ultimately proven to be borne on *Psaronius* stems or upon stems of intermediate structure between *Psaronius* and certain coenopterid stems.¹⁸

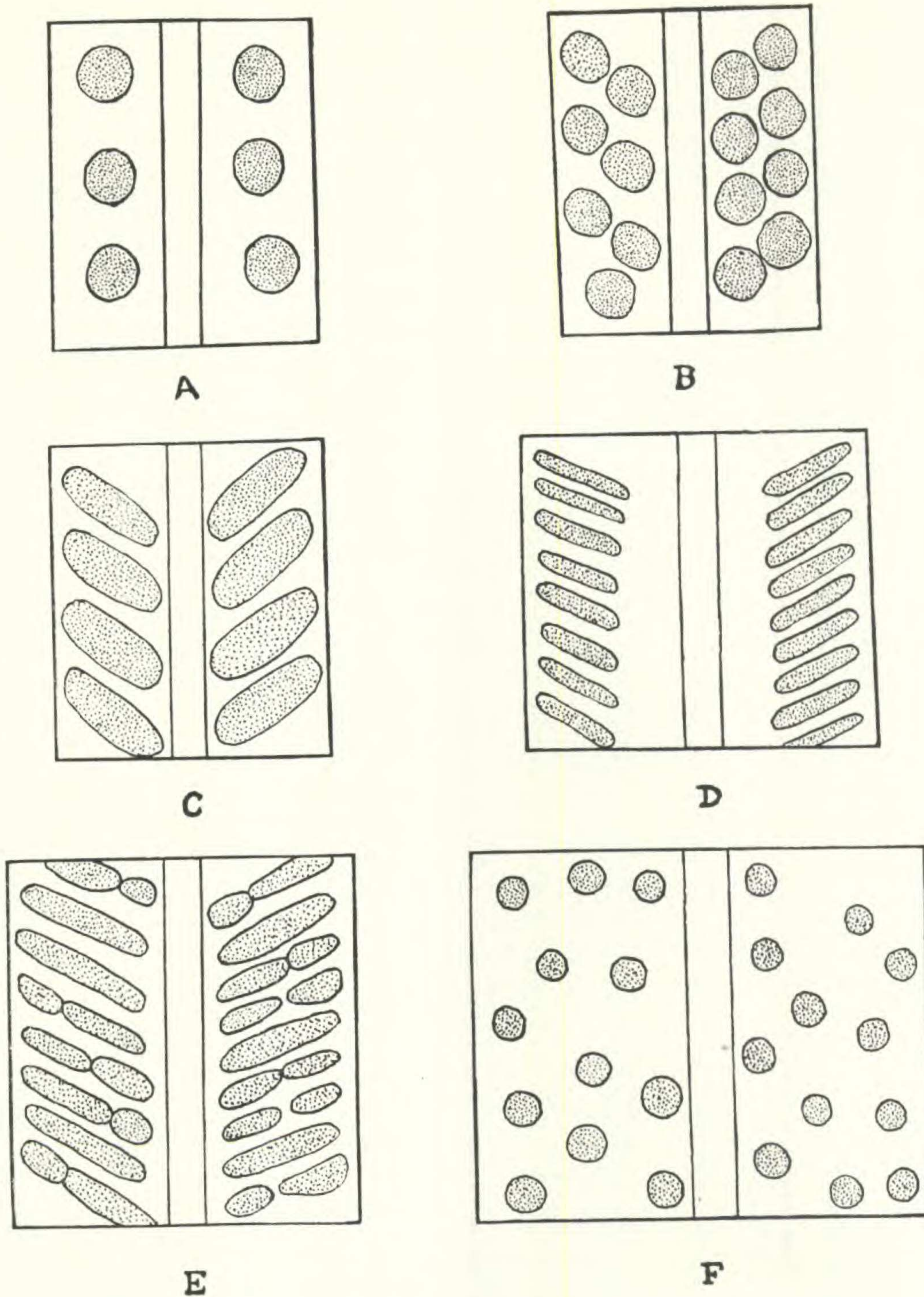
While the hazards of basing conclusions on the association of plant fragments are fully realized the bulk of the evidence uncovered to date strongly indicates a derivation of the fossil Marattiaceae from the anachoropterid coenopterids, involving the migration of the sori from the marginal to the superficial position, as diagrammed in text-fig. 4.

V. EVOLUTIONARY POSSIBILITIES AMONG THE MARATTIACEAE

A. THE DERIVATION OF LINEAR SORI

Upon the basis of the evidence uncovered during this work, we shall now consider the evolutionary possibilities within the Marattiaceae. One of the chief remaining problems lies in the derivation of the linear sorus, now predominant among the living Marattiaceae. Referring back to the description of *Scolecopteris*

¹⁸Lenz (1942) wrote: "This paper is intended as a further contribution to the apparent relationship between petioles described as *Anachoropteris* and *Stipitopteris* and fern stems described as *Psaronius* and *Caulopteris*."



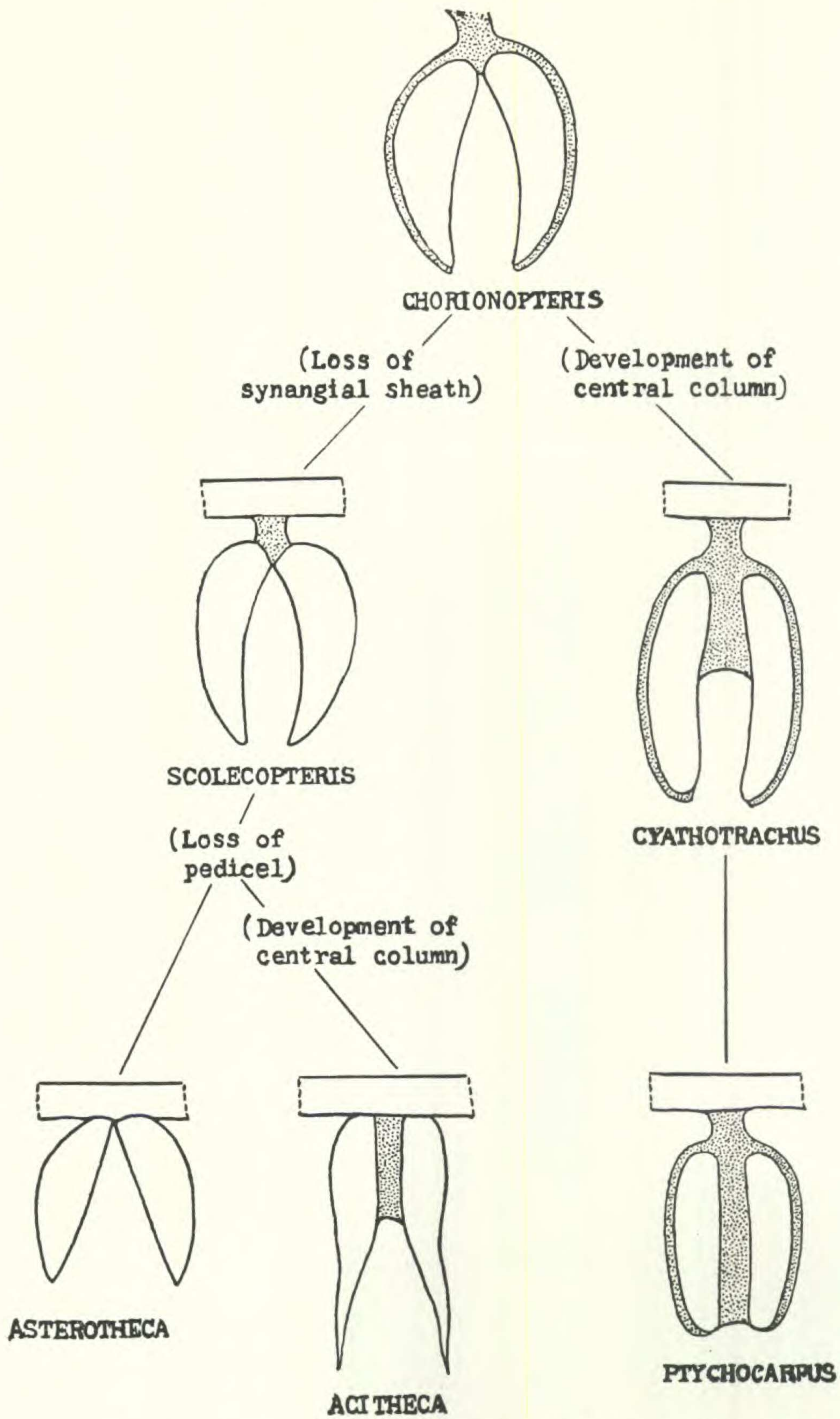
Text-fig. 5. Illustrating a possible sequence in the evolution of marattiaceous fungi: *A*, a typical asterothecous fructification, with the usual uniseriate condition; *B*, in which two rows of sori are borne on each side of the midrib, (sometimes seen in *Scolecopteris iowensis*); *C*, linear sorus such as in *Eoangiopteris* resulting from fusion of crowded radial sori such as shown in *B*. Expansion of the lamina might produce either of the two conditions: *D*, in which the sori are situated near the margins and away from the midrib (as in *Angiopteris*); or *E*, partial fission of the linear sori (sometimes seen in *Danaea*). Further expansion and fission might result in irregularly distributed radial sori as seen in *Christensenia* (*F*).

iowensis, a radial sorus, and *Eoangiopteris Andrewsii*, a linear sorus, certain similarities may be noted between the two fructifications. Individual sporangia of the two are similar in size, shape, and their dehiscence mechanisms. The tissues comprising the pedicel of *S. iowensis* and the receptacle of *E. Andrewsii* are alike. The spores of the two compare closely in gross morphology, size, and sculpturing of the exine. The chief difference between the two lies in the radial aspect of one as opposed to the linear aspect of the other.

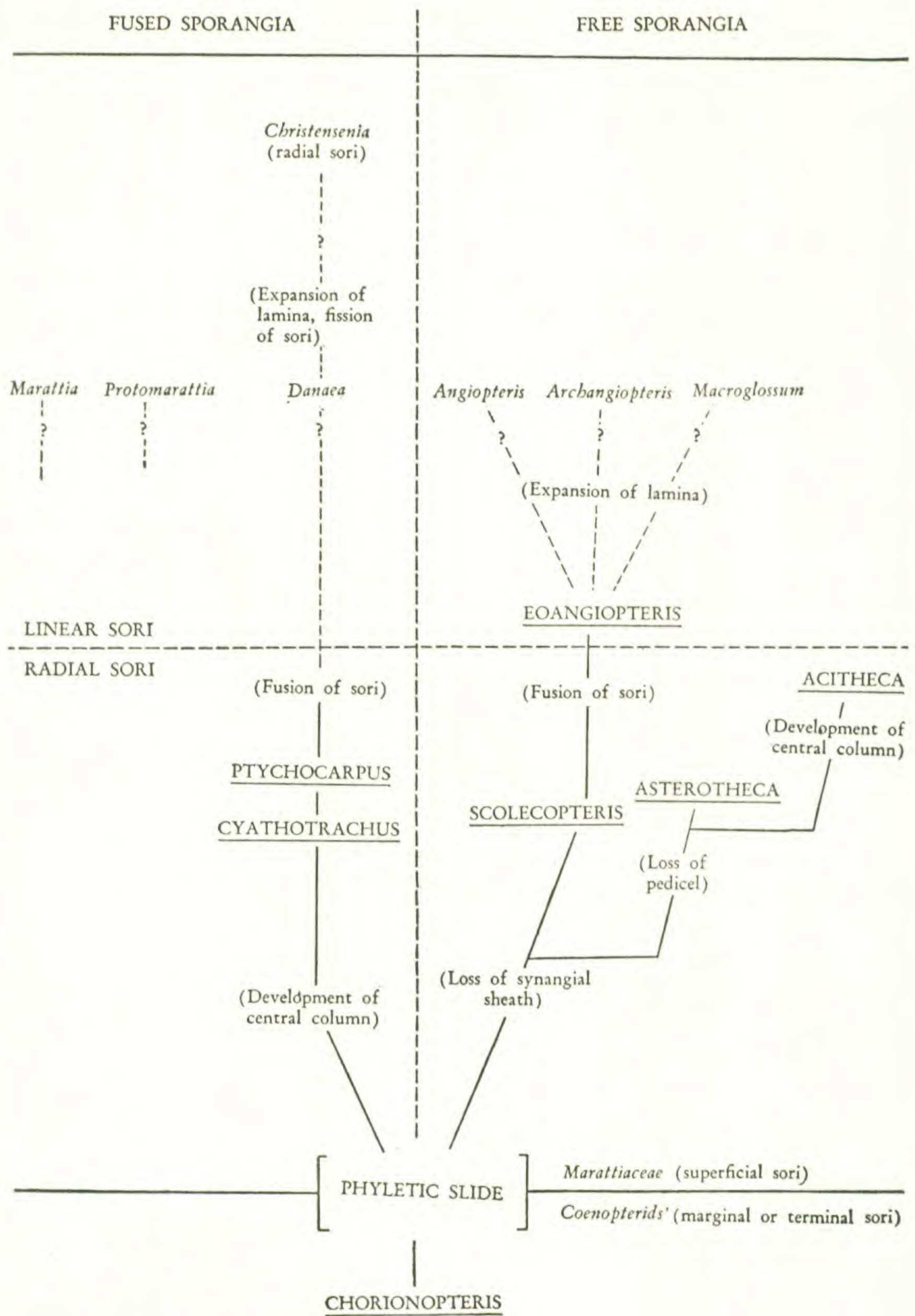
One feature of *S. iowensis* that deserves particular comment is that the fructifications are sometimes borne in *more than a single series* on each side of the midrib, resulting in an extremely crowded condition, as compared with the usual uniseriate arrangement found in other species. This suggests an ultimate *fusion* of sori along a lateral vein; eventual fusion of the pedicels would result in a linear, receptacular sorus such as that of *E. Andrewsii*. This process would allow for an increased sporangial production and more efficient utilization of the limited space provided by as small a pinnule as that which bore *E. Andrewsii*. While it is difficult to make a concrete statement concerning the evolutionary position of *S. iowensis* within the genus, its low spore output points to an advanced position among the known species, and it seems that this is in support of the *fusion* hypothesis offered above.

While it seems possible that *Eoangiopteris* was derived by *fusion* of radial sori and may have given rise eventually to the modern free-sporangiate linear sori of *Angiopteris*, *Archangiopteris*, and *Macroglossum*, the origin of the modern linear sori with fused sporangia remains in doubt. Conceivably the sori of *Danaea* may have evolved by a similar fusion of synangia of the *Ptychocarpus* type; an accompanying loss of the pedicel would result in a sorus similar to that of *Danaea*.

An interesting circumstance is to be noted in the relationship between pinnule size and fructification morphology. While the fossil fructifications were borne on very small, narrow pinnules and were crowded very closely together, the living Marattiaceae have relatively large, wide foliar segments with numerous but uncrowded sori. While the fossil sori are predominantly radial, the living ones are predominantly linear; thus it seems that the expansion of the lamina was accompanied by the development of linear fructification morphology, that is, *to a certain extent*. In this connection it is especially interesting to note that the modern genus *Christensenia*, considered to be the most advanced of the Marattiaceae by virtue of its dorsi-ventral habit, small size, large scales, highly expanded foliar segments and reticulate venation, produces *radial sori* which are very similar to the fossil sorus *Ptychocarpus*. Bower (1923) contends that the radial sori of *Christensenia* have been derived through the fission of a linear sorus of the *Danaea* type, accompanying an expansion of the lamina. Thus, if the proposed hypothesis of *soral fusion* may be considered a reasonable one, it appears that evolution of the marattiaceous sorus has undergone a complete reversal, with the archaic progenitors and most recent derivatives displaying essentially the same sort of soral morphology. This evolutionary sequence is diagrammed in text-fig. 5.



Text-fig. 6. Showing two possible lines of derivation of asterotheceous fructifications. Beginning with the coenopterid fructification *Chorionopteris*, the line of development shown at the right involves development of a central column and results in asterotheceous sori with *fused* sporangia. The line of development shown at the left involving loss of the synangial sheath, loss of the pedicel, and development of a central column, results in asterotheceous sori with *free* sporangia.



Text-fig. 7. A proposed phyletic chart of the Marattiaceae.

B. THE DERIVATION OF THE VARIOUS RADIAL SORI

Returning to the fructification *Chorionopteris*, it appears that as a progenitor for the asterotheceous fructifications, only a few minor evolutionary alterations are necessary to produce the latter several types. These fall into two distinct lines (see text-fig. 6).¹⁹ Although *A*, *B*, *C*, and *D* involve free-sporangiate sori, while *E* and *F* represent sori with fused sporangia, a complete series such as illustrated might have been accomplished within either the fused- or free-sporangiate soral groups.

1. By retention of the pedicel and synangial sheath, along with the development of a central column, the *Ptychocarpus* type might be produced, with *Cyatbotrachus* as an intermediate.

2. By reduction of the synangial sheath, the *Scolecopteris* and *Asterotheca* types might be derived, depending upon the simultaneous retention or reduction of the pedicel. By the development of a central column in a fructification of the *Asterotheca* type, an *Acitbeca*-like fructification might be derived.

The above evolutionary processes, along with that presented in text-fig. 4, would result in the above-mentioned soral types, in the superficial position. It thus appears that pedicellate sori with fused sporangia represent the most primitive type, with sessile, free-sporangiate forms advanced. (This is in direct opposition to the series proposed by Graham (1934), in which sessile forms are considered to be primitive.)

The Marattiaceae are proposed as having been derived from the coenopterid ferns, involving a "phyletic slide" in which the coenopterid genus *Chorionopteris* is the primitive form (text-fig. 4). The superficial marattiaceous sori appear to have developed along two distinct lines: those with fused sporangia placed at the left of the vertical broken line, and those with free sporangia at the right (text-fig. 6). Within each of these two groups are found both the primitive *radial* sori (placed below the horizontal broken line) and the apparently derived *linear* sori (above that line). Although *Christensenia* produces radial sori, it is apparently the most highly evolved form and consequently occupies the highest position among genera with fused sporangia. All fossil genera are underlined in this chart. While future work in the field of coal ball research will undoubtedly modify the phylogenetic trends suggested in the foregoing pages and diagrammed in text-fig. 7, such discoveries are eagerly awaited by the author with the hope that they will greatly amplify our knowledge of the past history of this interesting group of ferns. Any criticisms or suggestions will be gratefully accepted.

ACKNOWLEDGMENT

The author wishes to express appreciation of the many valuable suggestions of Dr. Henry N. Andrews, under whose direction the present work was accomplished. Thanks are also due the Director of the Missouri Botanical Garden for making

¹⁹Because of its apical annulus, the genus *Sturiella* is of doubtful affinity and is not considered here.

available the library facilities, and Dr. Rolla Tryon, for offering constructive suggestions during the course of this work.

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EXPLANATION OF PLATE

PLATE 1

Figs. 1-4. *Botryopteris fecunda*

Fig. 1. A group of three sporangia, sectioned longitudinally. The pedicel of the sporangium at the left may be seen at the top of the figure. Slide #1680, $\times 100$.

Fig. 2. Two sporangia, sectioned transversely. Note the annulus-like differential thickening of the sporangial walls. Slide #1680, $\times 120$.

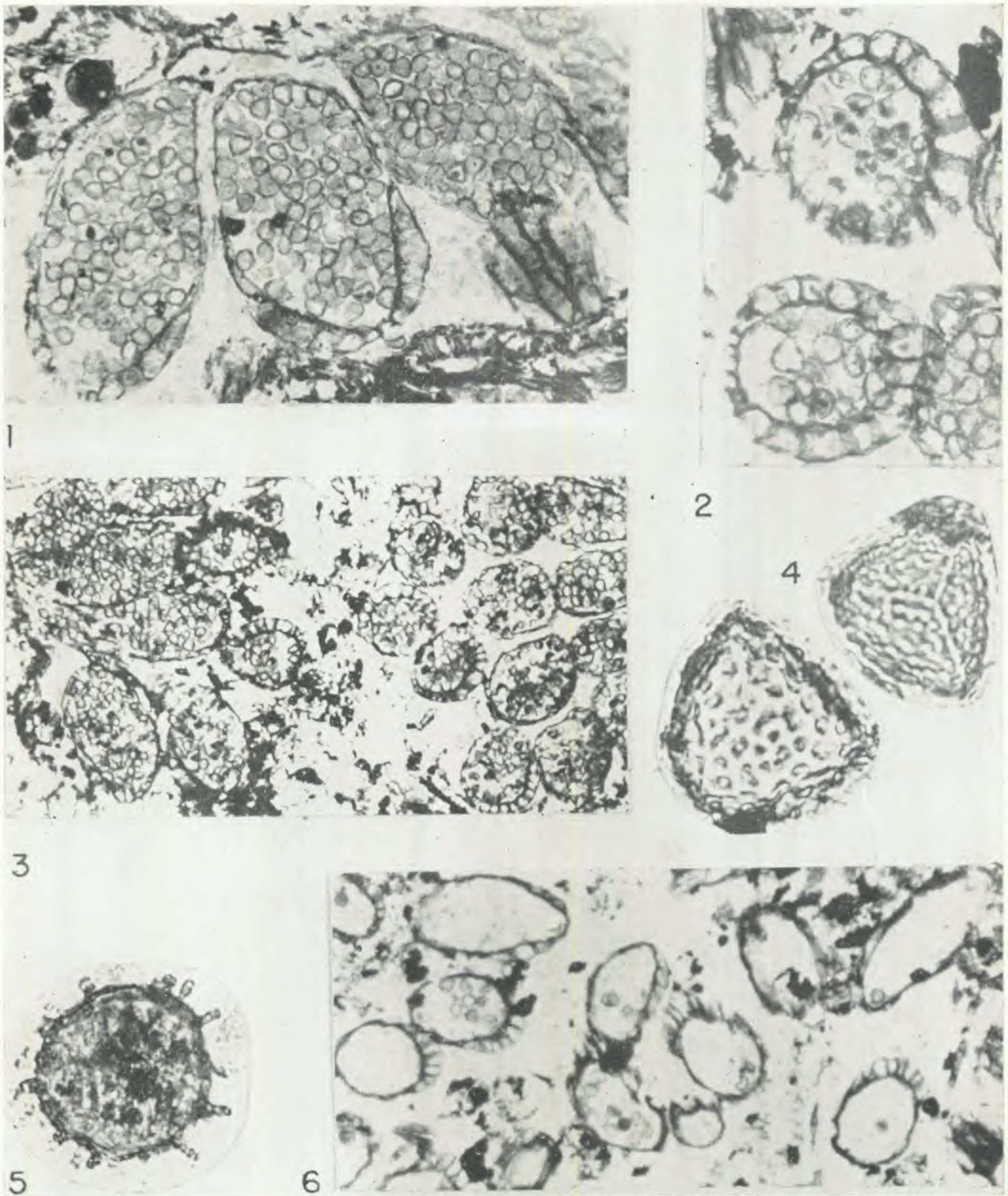
Fig. 3. A group of closely crowded sporangia, sectioned both transversely and longitudinally. Slide #1680, $\times 53$.

Fig. 4. Spores. Note the tetrahedral shape and triradiate ridge. Slide #1680, $\times 700$.

Figs. 5, 6. *Botryopteris spinosa*

Fig. 5. Spore. Note the blunt spine-like projections. Slide #1683, $\times 500$.

Fig. 6. A group of loosely aggregated sporangia, sectioned both transversely and longitudinally. Slide #1683, $\times 45$.



MAMAY—FERN FRUCTIFICATIONS

EXPLANATION OF PLATE

PLATE 2

Figs. 7, 8. *Botryopteris spinosa*

Fig. 7. A group of sporangia, the largest one sectioned longitudinally. Note the short pedicel at the upper right. Slide #1683, $\times 135$.

Fig. 8. Two sporangia, sectioned transversely. Note the thin sporangial walls, with annulus-like thickenings. Slide #1683, $\times 155$.

Figs. 9, 10. *Botryopteris illinoensis*

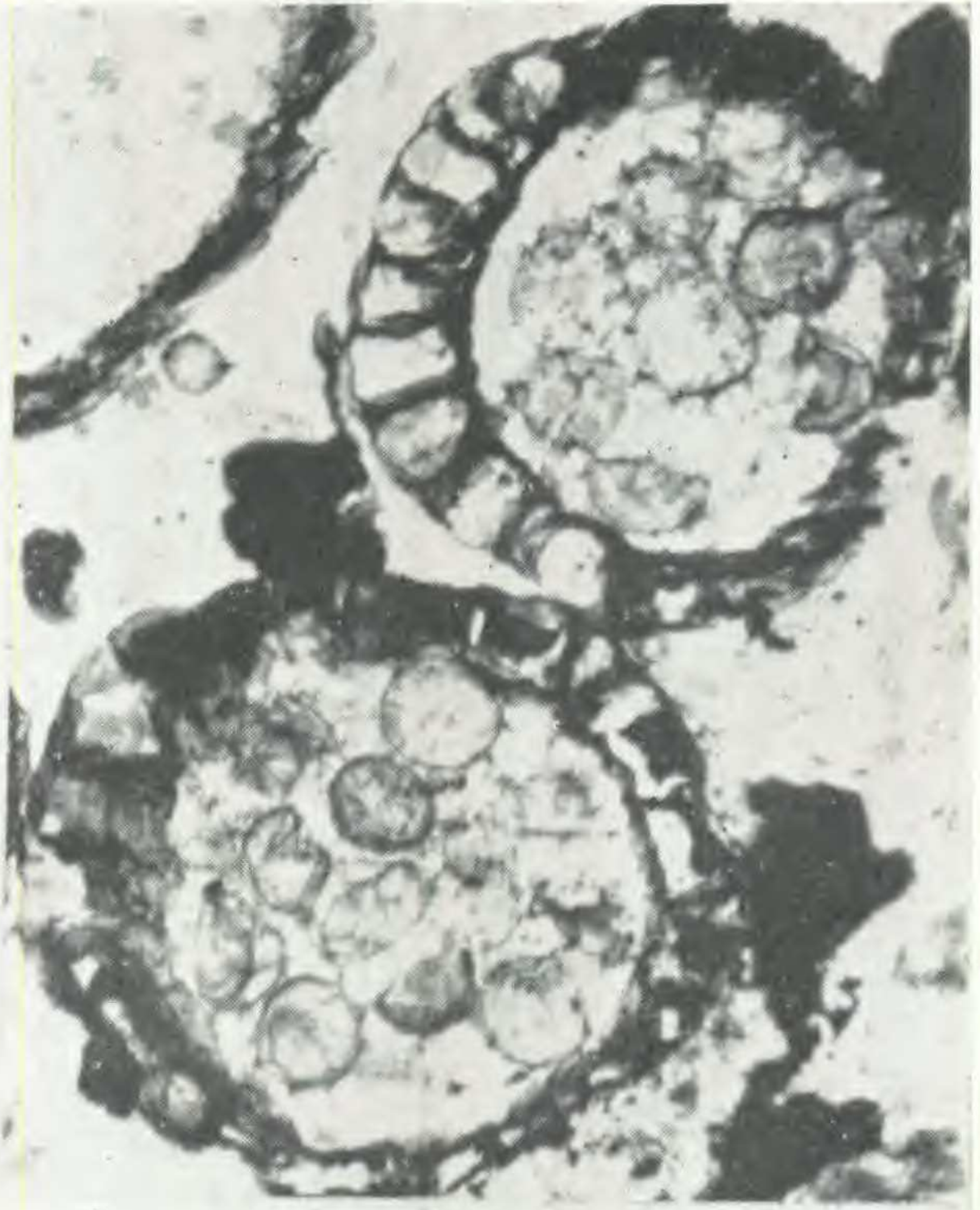
Fig. 9. Spores. Slide #1685, $\times 1360$.

Fig. 10. A single sporangium, sectioned transversely. Note the markedly differential thickening of the sporangial wall, which is a single cell in thickness. Slide #1686, $\times 165$.

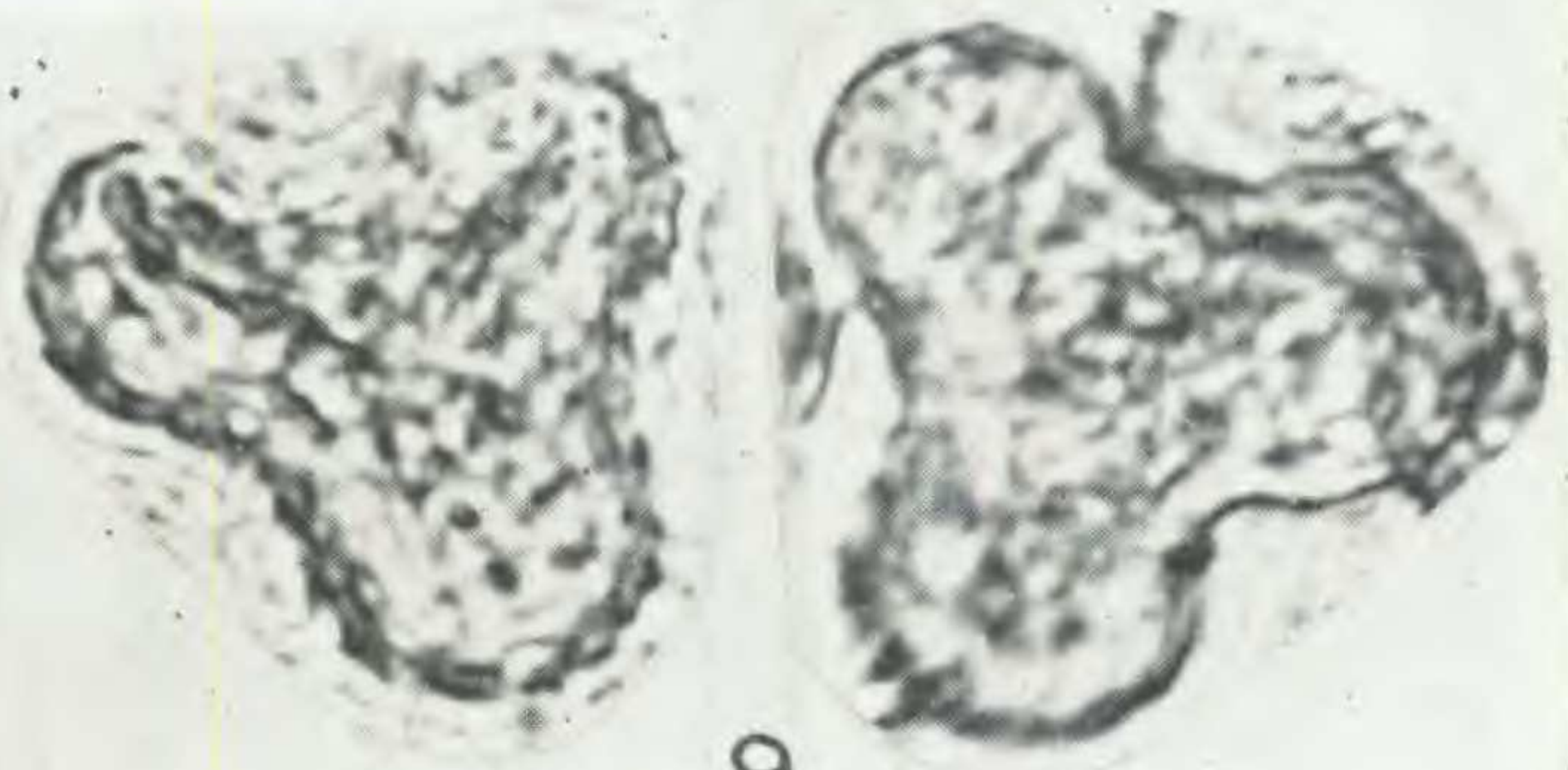
Fig. 11. *Ptychocarpus unitus* Brongniart. A single synangium, sectioned transversely. *a*, bundle of receptacle; *b*, its parenchyma; *c*, tapetum; *d*, spores; *e*, *f*, common envelope of synangium. Figure and explanation from Bower, after Renault, $\times 60$.



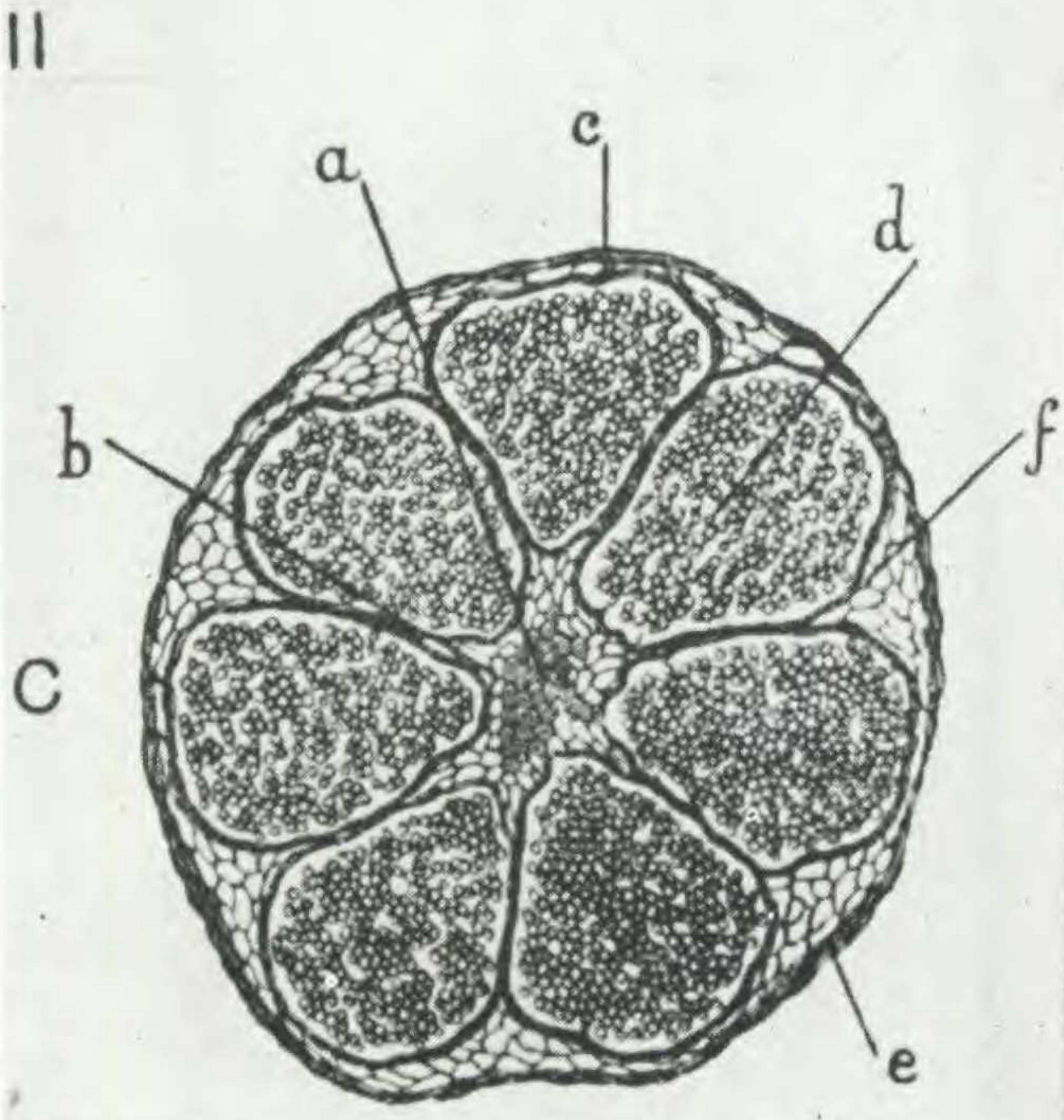
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MAMAY—FERN FRUCTIFICATIONS

EXPLANATION OF PLATE

PLATE 3

Cyatbotrachus altissimus

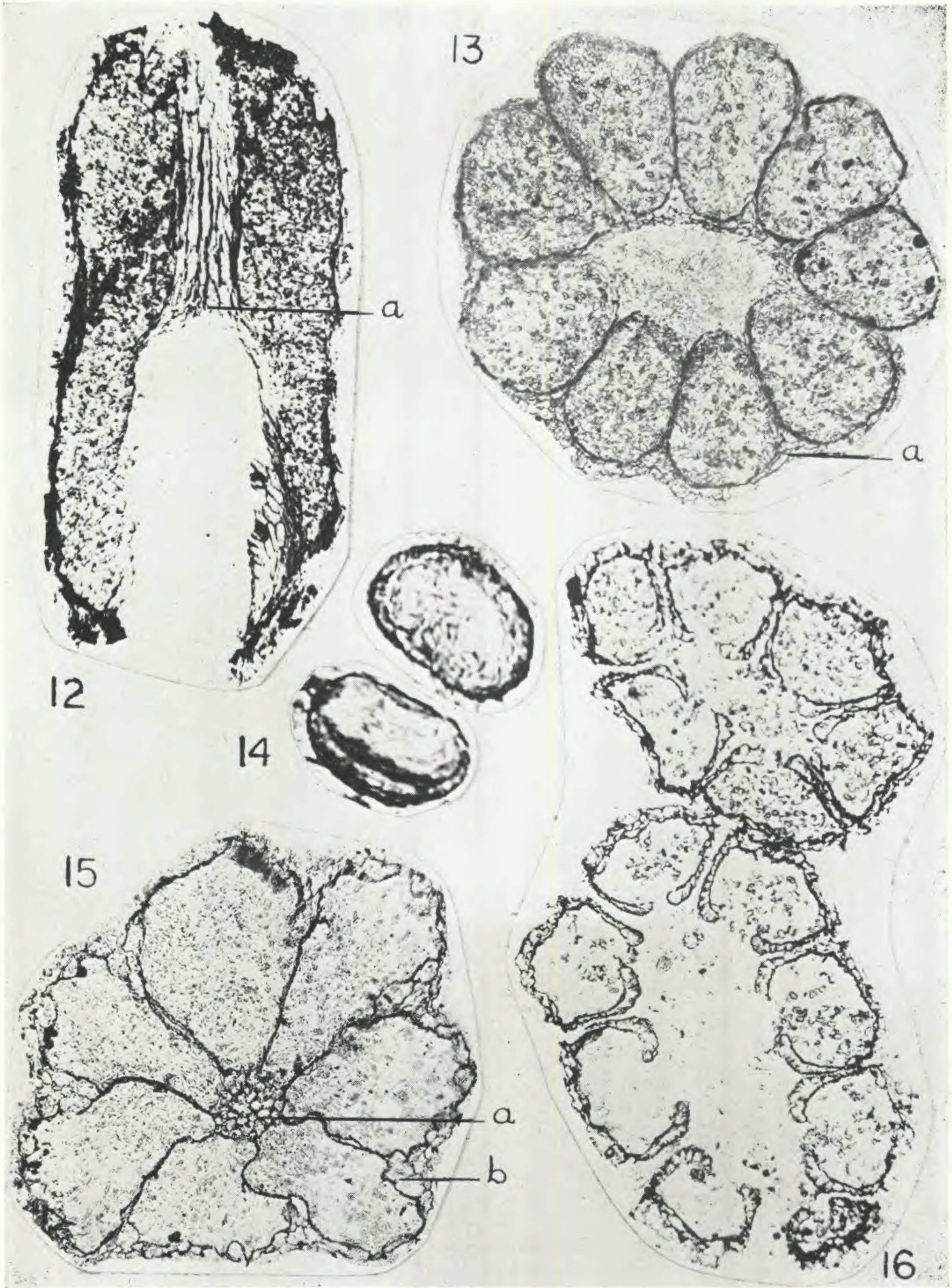
Fig. 12. A single synangium, sectioned longitudinally. Note the hollow cup-like portion of the fructification, extending distally from the termination of the central column (*a*). Slide #1687, $\times 50$.

Fig. 13. A single synangium, sectioned transversely through its hollow cup-like portion, with spore masses intact. *a*, continuous synangial wall (compare with *e*, *f*, fig. 11). Slide #1692, $\times 60$.

Fig. 14. Spores. Slide #1688, $\times 1300$.

Fig. 15. A single synangium, sectioned transversely through the central column. *a*, central column; *b*, synangial wall. Slide #1688, $\times 60$.

Fig. 16. Two dehiscent synangia, sectioned transversely. Note that the sporangia have separated from each other and display slits of dehiscence at their innermost surfaces. Slide #1688, $\times 70$.



MAMAY—FERN FRUCTIFICATIONS

EXPLANATION OF PLATE

PLATE 4

Scolecopteris latifolia

Fig. 17. Two pinnules, transversely sectioned, with attached synangia. Note the broad, strongly inflexed margins of the pinnules. Slide #1697, $\times 15$.

Fig. 18. A pinnule sectioned parallel to the plane of the lamina, with several synangia shown sectioned transversely. Note the predominance of trilocular synangia, and the dense black contents of the cells of the epidermis and hypodermis (*a*). Slide #1694, $\times 18$.

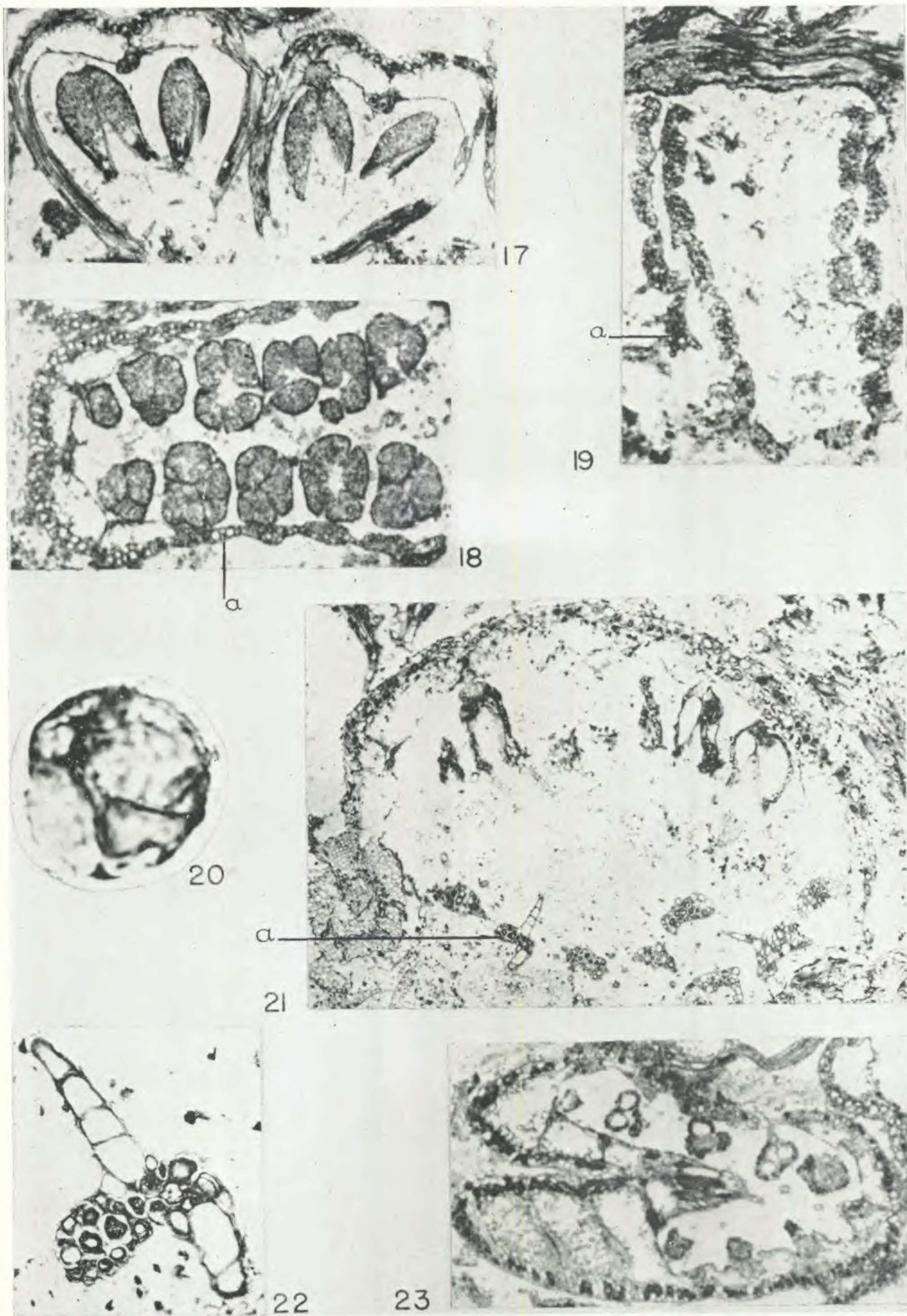
Fig. 19. A single pinnule and portions of the margins of two adjacent ones, sectioned in a plane paralleling that of the lamina, but below the apices of the fructifications. The penultimate midrib is shown at the upper portion of the figure. Note that the inflexed pinnule margins are dissected, appearing as series of separate crescent-shaped bodies with dense cellular contents. *a*, a single lobe of the pinnule margin. Slide #1694, $\times 16$.

Fig. 20. Spore. Slide #1697, $\times 800$.

Fig. 21. A single pinnule, sectioned in a plane parallel to its midrib, but near one "shoulder" of the pinnule, with the section intercepting several of the attached synangia. The penultimate midrib is shown at the left, transversely sectioned. At the bottom of the figure are shown transverse sections of the strongly inflexed marginal lobes, one of which is indicated at point *a*. Slide #1696, $\times 17$.

Fig. 22. Higher magnification of the lobe seen in figure 21, *a*. Note the epidermal hairs and the dense cellular contents. Slide #1696, $\times 70$.

Fig. 23. A single pinnule, sectioned parallel to the plane of the lamina. A portion of the midrib and several of the lateral veins are shown, along with several synangia, sectioned transversely near their bases. The hypodermis appears as a nearly continuous black outline to the pinnule. Slide #1694, $\times 17$.



MAMAY—FERN FRUCTIFICATIONS

EXPLANATION OF PLATE

PLATE 5

Scolecoperis iowensis

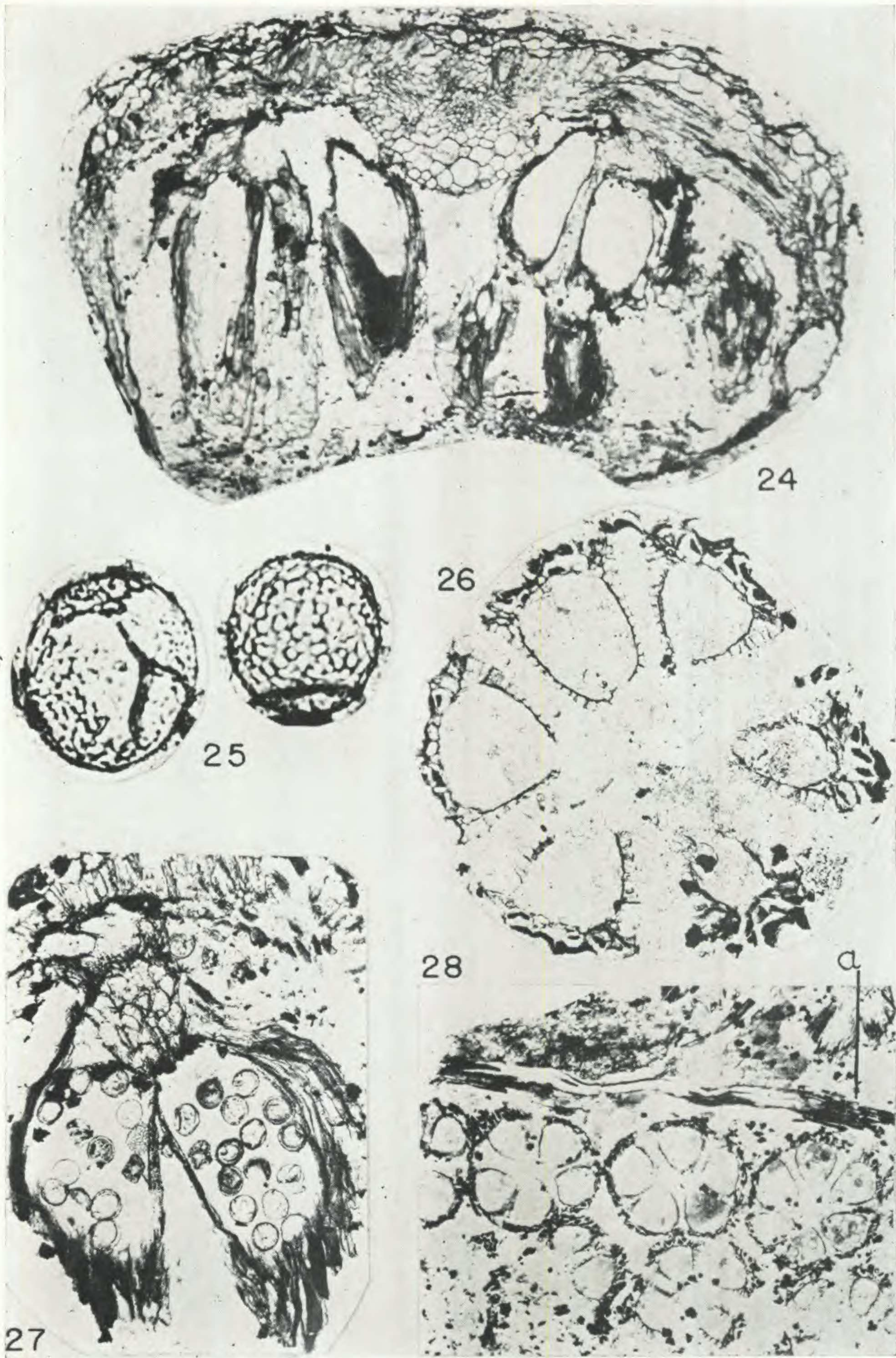
Fig. 24. Transverse section of a pinnule, with fructifications attached. Note the strong midrib and inflexed pinnule margins. Slide #1698, $\times 36$.

Fig. 25. Spores. Note the reticulate exines and triradiate ridge. Slide #1702, $\times 350$.

Fig. 26. Transverse section of a synangium containing six sporangia. Note the dense cellular contents of the outer walls, and the thin inner sporangial walls. Slits of dehiscence are evident at the innermost portion of each sporangial wall. Slide #1702, $\times 74$.

Fig. 27. Longitudinal section of a synangium, showing its pedicellate attachment to the pinnule. Slide #1698, $\times 60$.

Fig. 28. Portion of a pinnule, sectioned in a plane paralleling the lamina. At one side of the midrib (*a*) are shown two closely appressed rows of synangia. Slide #1702, $\times 20$.



MAMAY—FERN FRUCTIFICATIONS

EXPLANATION OF PLATE

PLATE 6

Scolecopteris minor Hoskins var. *parvifolia* Mamay

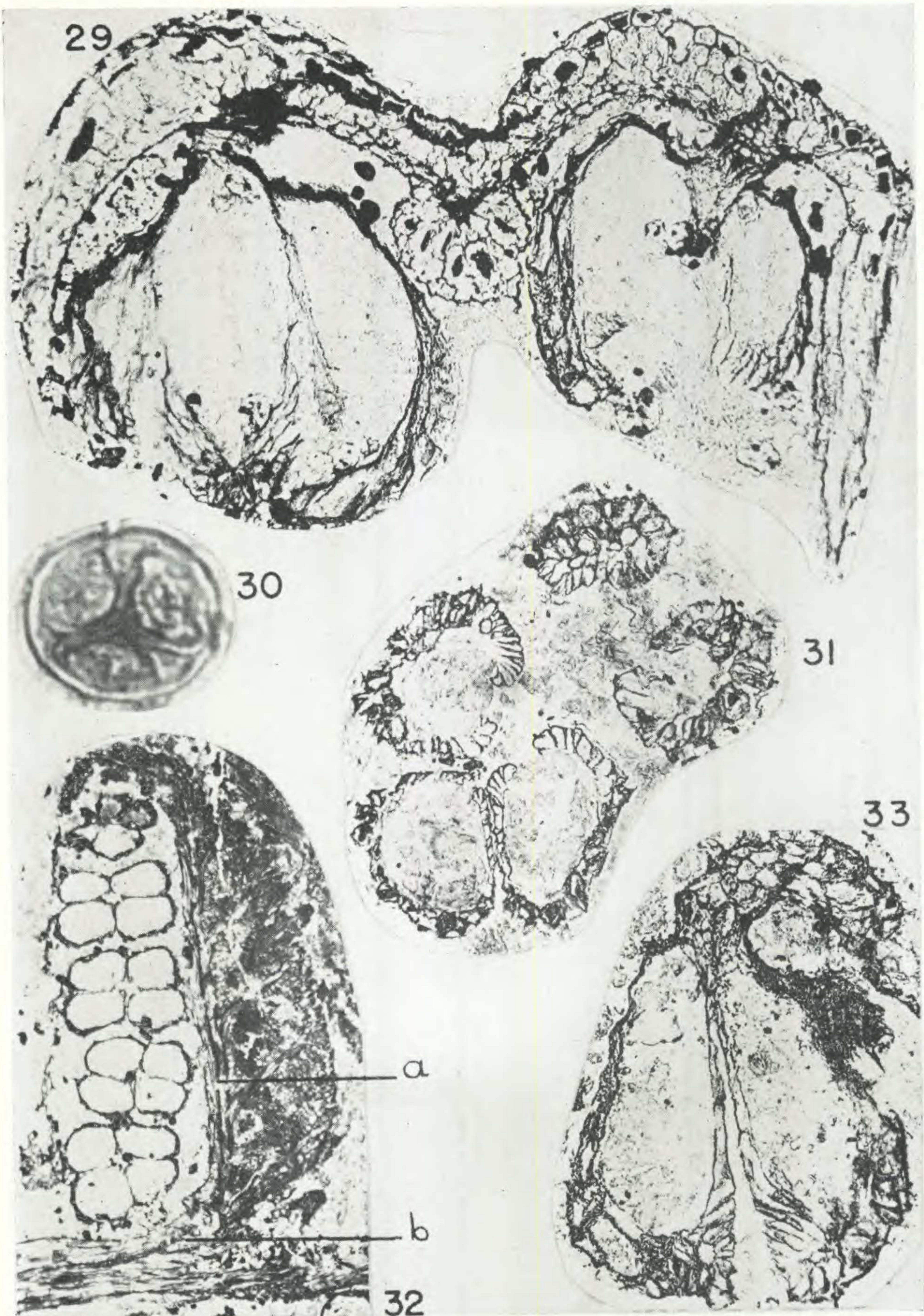
Fig. 29. Transverse section of a pinnule with two synangia attached. Note the strong midrib and inflexed pinnule margins. Slide #1704, $\times 66$.

Fig. 30. Spore. Note the triradiate ridge. Slide #1703, $\times 1650$.

Fig. 31. Transverse section of a synangium containing five sporangia. Slide #1708, $\times 66$.

Fig. 32. Pinnule sectioned in a plane paralleling the plane of the lamina. The midrib (*a*) is seen departing from the penultimate midrib (*b*). To the right of the pinnule midrib, several lateral veins are shown; to the left, five synangia are shown in transverse section. Slide #1706, $\times 20$.

Fig. 33. Longitudinal section of a synangium, showing the pedicellate attachment to the lamina. Slide #1708, $\times 80$.



MAMAY—FERN FRUCTIFICATIONS

EXPLANATION OF PLATE

PLATE 7

Scolecoperis incisifolia

Fig. 34. Portion of a pinnule sectioned in a plane parallel to the midrib and at right angles to the plane of the lamina (this approximates the section shown in diagram C, text-fig. 1). The lamina proper is shown at the upper portion of the figure (*a*); below this are shown four synangia, transversely sectioned (*b*); below the synangia are several of the inflexed lobes of the pinnule margin (*c*). Slide #1709, $\times 45$.

Fig. 35. Two immature synangia, longitudinally sectioned. Note the vascularized pedicels (*a*). Slide #1709, $\times 55$.

Fig. 36. Transverse section of a lobe of the pinnule margin. Slide #1709, $\times 100$.

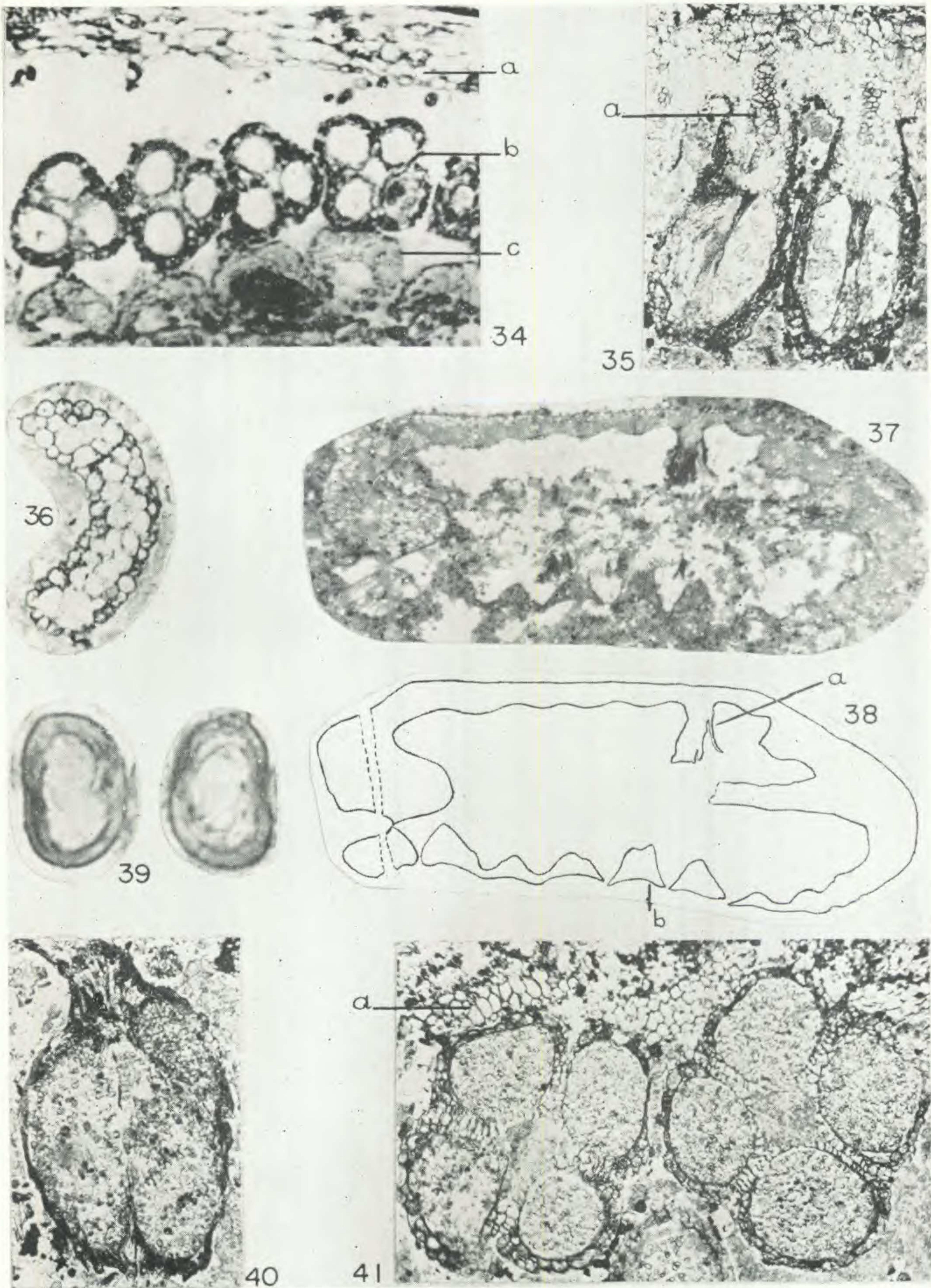
Fig. 37. Pinnule sectioned in a plane parallel to that of the lamina. (For clarification see fig. 38.) Slide #1712, $\times 18$.

Fig. 38. Line drawing of the pinnule section shown in fig. 37. A portion of the midrib is shown at the right. The inflexed pinnule margin at the upper portion of the drawing is shown as a continuous tissue, with portion of a synangium attached (*a*). The opposite margin has been sectioned in a slightly lower plane, and is seen to be dissected. A marginal lobe is shown at point *b*.

Fig. 39. Spores. Note the thick spore walls. Slide #1711, $\times 1000$.

Fig. 40. Longitudinal section of a synangium. Slide #1711, $\times 75$.

Fig. 41. Transverse section of two synangia, each containing four sporangia. *a*, inflexed lobe of pinnule margin. Slide #1711, $\times 55$.



MAMAY—FERN FRUCTIFICATIONS

EXPLANATION OF PLATE

PLATE 8

Scolecopteris major

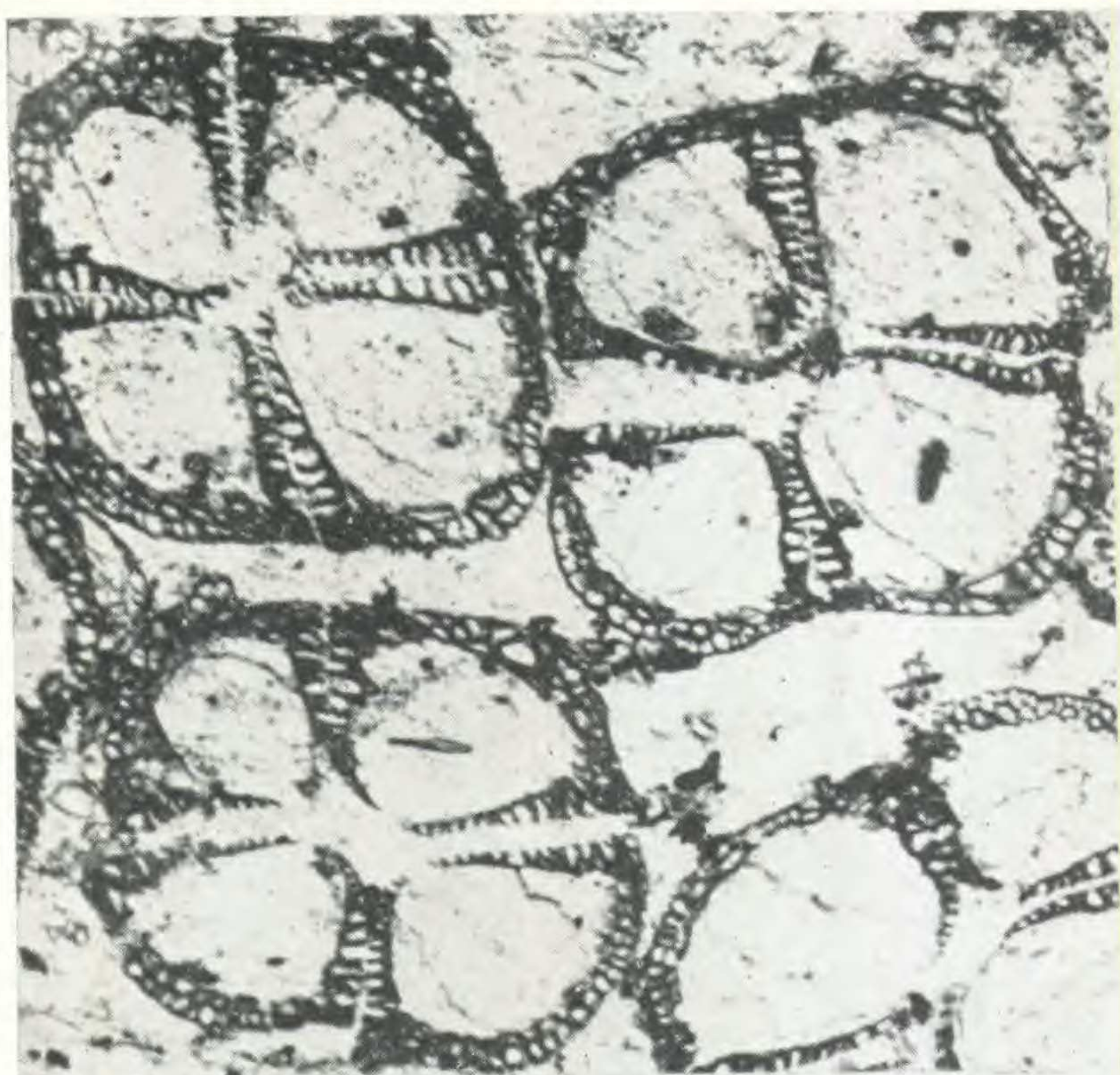
Fig. 42. Transversely sectioned synangia, each containing four sporangia. Note the thick outer walls of the sporangia and the slits of dehiscence along the innermost surfaces of the sporangia. Slide #1717, $\times 50$.

Fig. 43. Longitudinal-transverse section of a synangium. The two sporangia in the upper portion of the figure are shown in transverse section; the two remaining sporangia are shown in a three-dimensional (longitudinal-transverse) view. Slide #1717, $\times 50$.

Fig. 44. Longitudinal section of a synangium. Note the short, thick pedicel. Slide #1714, $\times 36$.

Fig. 45. Spores. Note the thick triradiate ridge. Slide #1713, $\times 450$.

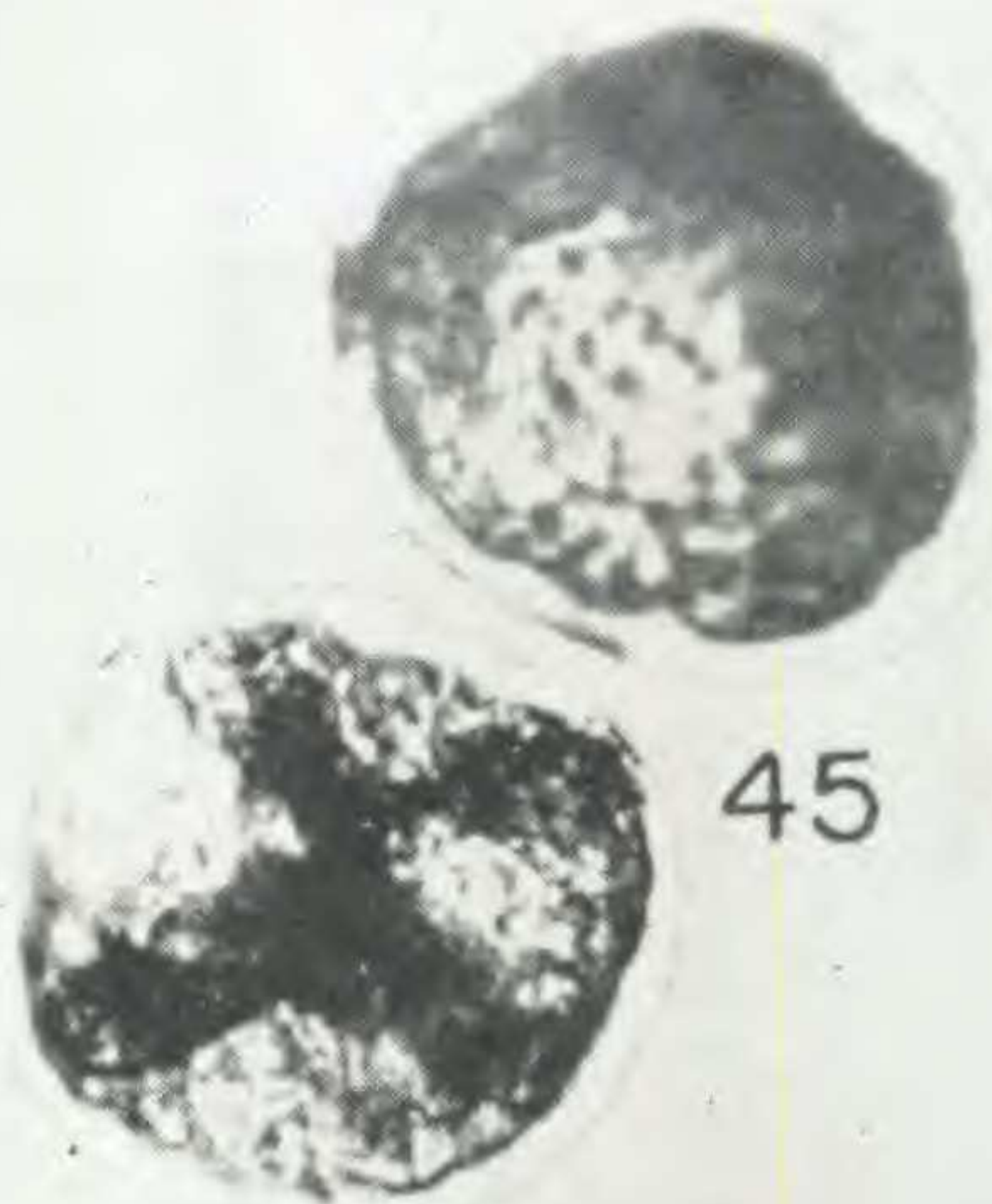
Fig. 46. Apex of a sporangium, showing two multicellular hairs attached. Slide #1715, $\times 100$.



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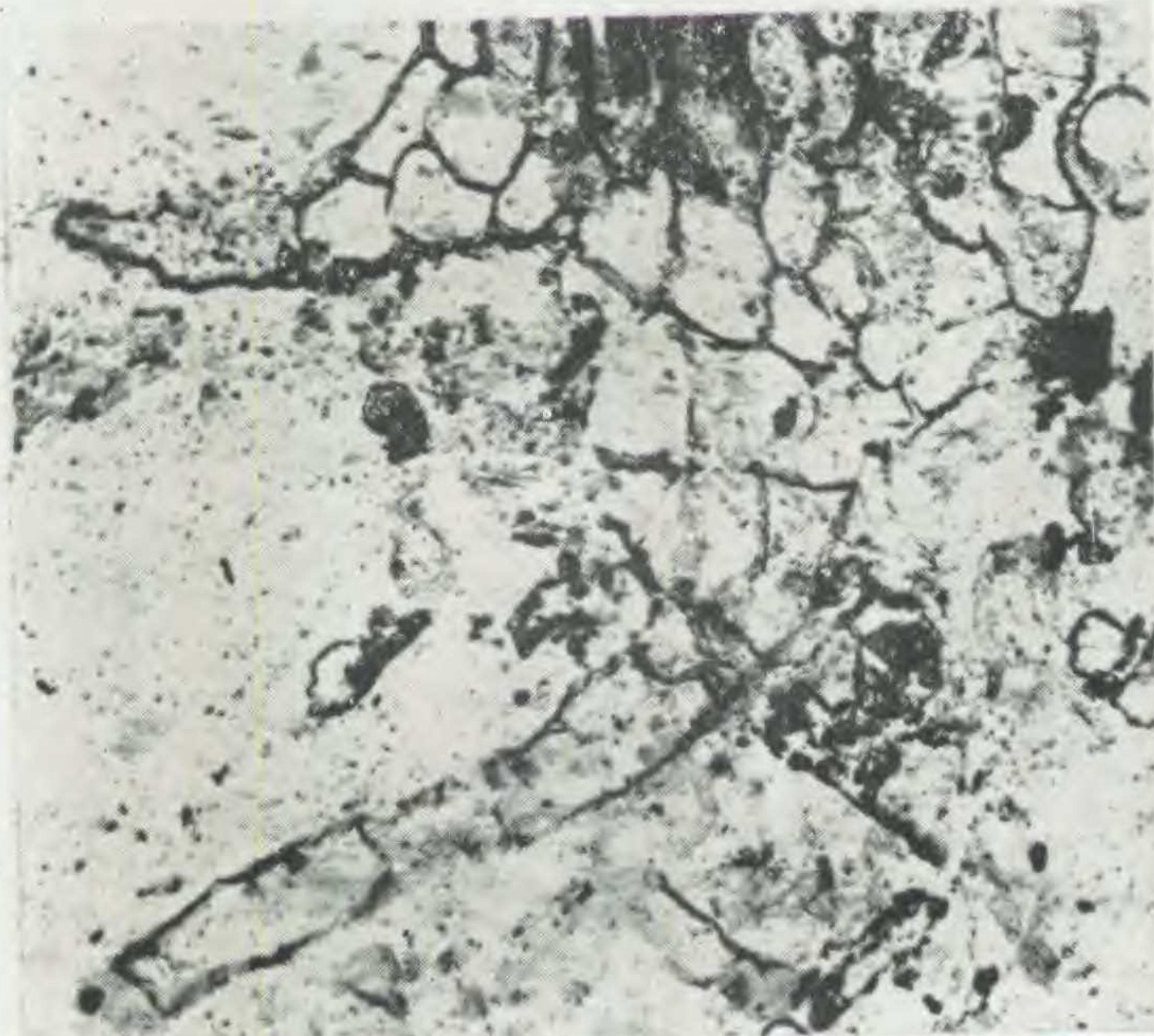
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EXPLANATION OF PLATE

PLATE 9

Eoangiopteris Andrewsii

Fig. 47. A pinnule sectioned in a plane parallel to that of the lamina, and slightly below it. The midrib (*a*) and several synangia are shown. Slide #1723, $\times 20$.

Fig. 48. Two synangia. *a*, inflexed pinnule margin; *b*, receptacle of synangium. (For clarification of this section see text-fig. 2, D, which approximates the section shown in fig. 48, represents a section cut through plane *b-b'* of diagram B.) Slide #1720, $\times 54$.

Fig. 49. Transverse section of a synangium. *a*, receptacle. (For clarification of this and fig. 50, see text-fig. 2, C, which represents a section taken through plane *a-a'* of B. The receptacle is stippled.) Slide # 1723, $\times 52$.

Fig. 50. Transverse section of a synangium, taken in a plane above the receptacle. Note the slits of dehiscence along the innermost surfaces of the sporangia. Slide #1719, $\times 53$.

Fig. 51. Longitudinal section of synangium. *a*, receptacle. Slide #1722, $\times 40$.

Fig. 52. Spore. Note the reticulate exine. Slide #1719, $\times 370$.

Fig. 53. Transverse section of a pinnule midrib. *a*, u-shaped vascular bundle; *b*, multicellular hair. Slide #1726, $\times 50$.